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VEGETATION OF THE GREAT SALT LAKE REGION

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 450

SEVILLE FLOWERS

(WITH ONE FIGURE)

Origin of Great Salt Lake

Great Salt Lake is located in northwestern Utah and is the remnant of Lake Bonneville, a great body of fresh water extant in Pleistocene times. At its highest level the ancient lake stood about 1000 feet above the present level of Great Salt Lake. A slight rise in level caused it to overflow its rim at a point since known as Red Rock Pass, Idaho. The outlet was eroded at a rapid rate with the subsequent lowering of the lake level. Erosion continued for 375 feet, when a large mass of hard rock was encountered. At this time the lake is believed to have had a longer period of constant level than at any other period in its history. Further decline of the lake was due to evaporation. At a point 200 feet above the present level of Great Salt Lake, alkaline salts began to concentrate and were deposited in the sediments. Evidences of the extinct lake are manifested mainly in the terraces and alluvial fans high along the bases of the mountains. Two large terraces are very prominent, the Bonneville terrace, which marks the highest level, and the Provo terrace, which was formed when the rapid erosion of the outlet became arrested.

Physiography and geology

The topography of the region presents a series of parallel mountain ranges and valleys extending north and south, and cut diag-

onally by a series of passes so as to impart a somewhat latticed design to the region as a whole. Great Salt Lake occupies an area of coalescence of valleys and passes. To the east of the lake the Wasatch Mountains rise and constitute one of the principal watersheds of the basin. The Oquirrh and Stansbury mountains are short ranges lying directly south of the lake.

The greatest extent of the lake shore is bordered by lowlands. The valley floors are composed of lacustrine sediments dominated by clays and loams. The depth of the valley fill has not been determined definitely, but wells have been sunk to a depth exceeding 2000 feet and the deposits have been found to be remarkably similar, both vertically and horizontally. Extending from the lake the following soil series is recognized: Great Salt Lake sand, Jordan clay, Jordan sand, Jordan sandy loam, Jordan loam, Bingham loam, and Bingham gravelly loam. The Jordan series is notably alkali-bearing.

The mountains rise abruptly from the floor of the valley in many places, but long alluvial slopes, called bajadas, extend for 1 to 5 miles, gradually rising to an elevation of nearly 1550 feet above the bottom of the valley. Old lake terraces high along the bases of the mountains are a conspicuous topographical feature.

Practically all of the permanent streams reaching the lake arise to the east. Three rivers, the Bear, Weber, and Jordan, carry the greatest amount of drainage water. Numerous smaller streams enter directly. The southern, western, and northern sections contribute almost no surface water other than flood run-off. Springs are common along the bases of the mountains and along the lake shore, while permanent wells have been sunk at various points.

Climate

Precipitation and temperature data were taken from representative stations surrounding the lake. Additional data were obtained from other stations. Stations located near the base of high mountains show the highest average rainfall while the valley and desert stations show the lowest amounts. Corinne, Ogden, Farmington, and Saltair are located on the eastern side of the lake, Midlake is on the Southern Pacific Railroad trestle in the middle of the lake, Kelton is located at the northwestern extremity 7 miles from the shore, and

Lemay is 20 miles west of the lake on the Great American Desert. The eastern section averages between 16 and 17 inches of rain per year, Farmington showing the highest annual mean of 20.67 inches and Corinne showing the lowest mean with 12.56 inches. The annual precipitation of the western section averages about 5.0 inches. Midlake shows 5.39 inches. Assuming that the data from these stations approach the averages of each section, there is about 10 inches difference between the western and eastern sides of the lake. The mean annual rainfall data are included in table I. Fragmentary data show

TABLE I

MEAN ANNUAL PRECIPITATION, TEMPERATURE DATA, AND LENGTH OF GROWING SEASON FROM GREAT SALT LAKE REGION

STATION	PRECIPITATION (INCHES)	TEMPERATURE (°F.)	LENGTH OF GROWING SEASON (DAYS)
Farmington	20.67	49.8	.....
Ogden	15.20	52.2	154
Corinne	12.56	50.4	.....
Saltair	14.51	50.7	193
Kelton	6.44	48.4	108
Lemay	4.32	51.1	174
Midlake	5.39	52.2	225

that the annual average for the mountains above 9000 feet elevation amounts to something between 28 and 40 inches. This is significant, as the contribution to the lake by way of streams depends upon the rainfall in the higher ranges.

The mean annual temperatures of the region show little variation and range from 48.4° to 52.2° F. The same stations furnished this datum as shown in table I.

There is a wide variation in the dates of the last killing frost in the spring and the first killing frost in the autumn. The averages of the dates recorded at each station furnish the approximate length of the growing season as shown in table I.

The only station within range of the lake where records of the relative humidity have been kept is located in Salt Lake City. The daily variation is very wide in the summer, ranging from 46% at 6:00 A.M. to 26% at 6:00 P.M. Table II shows the average monthly and annual percentages. Evaporation and wind movement data (table III)

were obtained from Midlake and Lehi, the latter station being located 25 miles south of Great Salt Lake.

According to the records taken in Salt Lake City, the sun shines 62.4% of the time possible for it to do so. The heaviest average amount occurs in July, with 80%. The average wind velocity in Salt Lake City is 7.8 miles per hour; the prevailing direction is southwest. The averages recorded here are taken from the records of the

TABLE II

AVERAGE MONTHLY AND ANNUAL HUMIDITY PERCENTAGES COVERING 31 YEARS IN SALT LAKE CITY

	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	ANNUAL
6 A.M.	75	73	65	69	57	50	46	46	49	58	65	73	59.7
6 P.M.	70	64	50	39	36	28	26	26	32	45	58	69	45.2

TABLE III

AVERAGE MONTHLY AND SEASONAL EVAPORATION IN INCHES AND WIND MOVEMENT IN MILES

	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	SEASON
Lehi									
Evaporation	5.533	8.583	9.957	10.412	9.455	6.776	3.887	1.502	56.752
Wind	3,972	4,119	3,664	3,039	3,161	2,633	2,671	2,433	29,458
Midlake									
Evaporation	6.815	11.888	8.310	14,369	13.612	6.908	5.753	3.888	68.677
Wind	7,794	9,204	8,030	7,731	5,945	7,983	6,306	5,727	69,139

Weather Bureau of the United States Department of Agriculture at Salt Lake City. With the exception of the evaporation data these records extend from 1879 to 1930.

Great Salt Lake

The actual shape and dimensions of Great Salt Lake are matters of no stable mean. The fluctuations in level from season to season and year to year alter the outline of the shore very materially and to a certain extent the dimensions. In general the long axis has a northwest-southeast trend. Its approximate size, according to the U.S. Geological Survey in 1906, is 75 miles long and 35 miles wide. The mean depth in 1929 was about 15 feet. The shape as represented on

the official maps of the Geological Survey shows it at its highest level, which was recorded in 1868. At that time the mean depth was 19 feet and all of the beaches exposed at the present time were submerged by at least 0.5 foot of water. This old shore line is well defined by a terrace ranging from 1 foot or less to 10 feet high. Throughout the ensuing discussions this shore line will be referred to as "the old shore line" or "the shore of 1868."

The deepest part of the lake is found in a trough which runs northwest-southeast between Antelope and Stansbury islands. The records of 1869 give the greatest depth as 49 feet; and with the great recession of 1903 measurements in a similar place showed only 36 feet, a difference of 16 feet, which corresponds to the difference in surface measurements.

The periodic oscillations have been measured over a period of nearly 75 years and on the average show a difference of 2 feet from the wet to the dry period. The level also fluctuates non-periodically chronologically. The level was first measured in 1850. In 1862 a permanent gauge was set up from which monthly readings were taken. Since records have been kept the lake has had one noticeable advance, followed by a recession, and in turn by another less pronounced advance; at present it is sinking again. The following are the important fluctuations:

1850..... 3 feet above the zero on gauge
1868.....14 feet above the zero on gauge
1874..... 8 feet above the zero on gauge
1877.....14 feet above the zero on gauge
1903..... 2 feet below the zero on gauge
1923..... 8 feet above the zero on gauge
1931..... 1 foot above the zero on gauge

The zero on the official gauge at Saltair stands at 4194.8 feet above sea level.

CHEMICAL CONSTITUENTS OF THE BRINE.—The waters of the lake have been analyzed repeatedly and the results are shown in table IV (2). The brines vary from 15 to 27.6% according to the level. In comparing the percentage of salts in the water with the fluctuation in level, it is found that there is approximately 1% increase in concentration for every foot decrease in level. This is relative, however,

since a very rapid recession of the lake often causes the salts to be precipitated in great masses of crystals instead of increasing the concentration very much. There are two sources of the salt, concentration of water from streams and contribution from hot mineral springs. The latter are 1–5% salt.

TABLE IV

ANALYSES OF GREAT SALT LAKE WATER (2)

	A	B	C	D	E	F
Cl	55.99	56.21	56.54	55.23	55.11	53.72
Br	Trace	.....	.....	Trace	.....	.....
SO_4	6.57	6.82	5.97	6.73	6.66	5.95
CO_3	.....	0.07	.....	.....	.....	.....
Li	Trace	.....	.....	Trace	.....	.....
Na	33.15	33.45	33.39	34.65	32.97	32.81
K	1.60	(?)	1.08	2.64	3.13	4.99
Ca	0.17	0.20	0.42	0.16	0.17	0.31
Mg	2.52	3.18	2.60	0.57	1.96	2.22
	100.00	100.00	100.00	100.00	100.00	100.00
Percentage salinity	14.904	13.790	19.538*	27.720	22.990	17.680

A. ALLEN, O. D., Rept. U.S. Geol. Expl. 40th Par. **2**:435. 1877. (Water collected 1869.)
B. SMART, CHARLES, cited in Resources and attractions of the Territory of Utah. (Collected 1877.)
C. TALMAGE, J. E., Science **14**:445. 1889. (Collected 1885.)
D. BLUM, W., Reported by TALMAGE in Scot. Geog. Mag. **20**:424. 1904. (Collected 1904.)
E. EBAUGH, W. C., and WILLIAMS, K., Chem. Zeitung. **32**:409. 1908. (Collected 1908.)
F. MACFARLANE, W., Science **32**:568. 1910. (Collected 1910.)

In comparison with other bodies of saline water, Great Salt Lake ranks among the most highly concentrated. The following tabulation shows the percentages of some of the saline lakes of Eurasia (3).

	Percentage salinity
Caspian Sea	1.294
Sea of Aral	1.084
Dead Sea	19.2 to 25.99
Red Lake, Perekop, Crimea	30.01
Gaukhane Lake, Persia	25.88

RECENT CONDITIONS.—The period extending from 1929 to 1931 exemplifies rather typical behavior of the lake. During the former year the level was 4–6 feet above the zero on the gauge and within 2 years receded almost to the zero mark, averaging about 1 foot above. It is obvious that bays and inlets fed by fresh-water tributaries have much less salt than the main body of the lake. Table V

TABLE V

PERCENTAGE TOTAL SALTS AND H-ION CONCENTRATION OF BRINES AT VARIOUS POINTS IN LAKE

LOCALITY	DATE	PERCENTAGE SALT	pH
Main body:			
Near Saltair	June 12, 1929	18.04	
Near Saltair	Aug. 30, 1931	20.50	8.2
North Point	June 12, 1929	18.06	
Near Jordan delta	July 29, 1929	15.71	
West Point	July 24, 1929	17.98	
West Farmington	Sept. 3, 1931	21.70	8.6
Little Mountain	June 29, 1929	18.01	
Bays and inlets:			
East Bay in swamp	June 17, 1929	1.03	
East Bay outer limits of swamp	June 17, 1929	5.86	
East Bay at Jordan delta	Sept. 8, 1931	10.60	8.2
Willard Spur, south side	July 8, 1929	11.68	
Willard Spur, north side	July 8, 1929	8.60	

gives the percentage total salts and H-ion concentration of water taken from representative situations.

The H-ion concentration of the brines is much the same in all parts of the lake. It is perhaps lower than might be expected in such a highly concentrated solution, but the strong buffer action of the weaker acid radicals checks the amount of dissociation. Even fresh waters of the same region have a pH of 8.2, so that there is little or no effect on this value when added to the lake waters.

Flora of Great Salt Lake

GENERAL FEATURES.—The water of Great Salt Lake is clear and transparent. In appearance there is nothing to distinguish it from a body of fresh water. Occasionally masses of algae form local colonies, imparting a brownish tinge to the water, and except in the bays

and inlets no emergent plants grow in it. The high saline constituents render the water toxic and unavailable for the use of most plants. On the lake borders and saline plains trees are absent, succulent herbs and low shrubs predominating. There are a few algae, lichens, and mosses but no liverworts nor pteridophytes. Hackberry and junipers make their closest approach on cliffs and sand dunes, willows occur along the rivers, and poplars have been introduced.

On the basis of salinity the flora of the lake waters may be divided into two general categories, that of the main body of the lake and that of the bays, inlets, and springs.

FLORA OF MAIN BODY OF LAKE.—Algae are the only plants that normally inhabit the main body of the lake where the salt reaches a high concentration. The following were collected:

Myxophyceae:
- Aphanothece utahensis Tilden[1]
- Microcystis packardii Farlow
- Oscillatoria tenuis var. natans (Kuetz.) Rab.
- O. tenuis var. tergestina (Kuetz.) Rab.

Chlorophyceae:
- Chlamydomonas sp.
- Tetraspora lubrica var. lacunosa Chauv.

Aphanothece utahensis is the dominant species at the present time. It floats on or near the surface in flaccid, rugose brown masses 4–6 inches in diameter. In local places it sometimes accumulates, imparting a brownish tinge to the water. It is rather evenly distributed in the deeper parts of the lake but is in greatest abundance along the eastern shore, on the eastern side of Stansbury Island, the northern and western sides of Antelope Island, and on the steep shores of the western side of the promontory. *Microcystis packardii* occurs in rather firm gelatinous masses 0.5–1 inch thick, usually spherical but often irregular in shape. The color is most frequently blue-green but brown and pale yellowish tints are common. The species of *Oscillatoria* are much less common and were encountered only occasionally.

[1] The manuals used in the identification of the plants mentioned in this paper were RYDBERG'S Flora of the Rocky Mountains, TIDESTROM'S Flora of Utah and Nevada, COULTER and NELSON'S Manual of Rocky Mountain Botany, LESQUEREUX and JAMES' Manual of North American Mosses, and BARNES and HEALD'S Key to the Genera and Species of Mosses.

All of the collections came from the eastern shore, where it forms thin layers on the muddy bottom in the still and shallow water. *Chlamydomonas* is abundant and fairly evenly distributed in the deeper parts but most common along the shores mentioned in connection with *Aphanothece*. *Tetraspora* floats in the brine along the quiet shores, growing in slimy olive-green masses. It is not common. Several diatoms were collected in the main body and a great many were taken from points where fresh water enters. Identifications were not obtained, but of the former group DAINES (4) says that two of them probably belong to the genera *Navicula* and *Cymbella*. DAINES also isolated in pure cultures five bacteria, four of which were bacilli and one diplococcus. No names are given.

Many other species of algae were taken from the main body of the lake, but the evidence seemed to indicate that they had been washed in from fresh-water situations. Among these are species of *Cladophora*, *Ulothrix*, *Spirogyra*, *Rhizoclonium*, *Enteromorpha plumosa*, and several others that could not be identified. PACKARD (9) reported the first account of the algae in Great Salt Lake in 1879. FARLOW identified the collections, among which he reported *Ulva marginata* Ag. and *Rhizoclonium salinum* Ktz. TILDEN distributed a series of algae from the lake which included *Enteromorpha marginata*, *E. tubulosa*, *Dichothrix utahensis*, and *Chara contraria*. In the present investigation none of these algae was found to be established inhabitants of the main body of the lake, but they grow abundantly in springs and brackish pools along the shore where the salt is greatly reduced in concentration.

FAUNA.—There are three species normally living in the lake water, the brine shrimp, *Artemia gracilis* Verrill, and two salt flies, *Ephydra gracilis* Packard and *E. hians* Say. These animals feed on the algae and are important in connection with the shore deposits.

EFFECTS OF ORGANISMS ON SEDIMENTATION.—The deposition of carbonate is of interest since the origin of this radical was obscure in view of the fact that the ordinary procedure of analysis of the lake water showed no carbonate radical. CAMERON (11) explains the cause of this as follows:

> There is sodium carbonate in solution, and normally this would dissociate with the formation of sodium ions, which could be detected with phenolphthalein but the water contains so large amount of salts with sodium ions that the solu-

tion is saturated with respect to this ion, and, carbonates being salts of a weak acid—that is, with a relatively small tendency to dissociate—the dissociation of the sodium carbonate is completely "driven back." Consequently there is no dissociation in the solution.

If the lake brine is diluted with distilled water, more sodium ions are permitted to enter solution, including those of sodium carbonate. At the same time the ions of the carbonate radical are permitted to go into solution and their presence may be detected with phenolphthalein.

The slightly soluble calcium sulphate occurring in the lake furnishes the calcium ions in the formation of calcium carbonate. This takes place by the forced solution of sodium carbonate resulting from the interaction between sodium chloride and calcium sulphate. The calcium and chlorine ions form calcium chloride, which is very soluble. This increases the solubility of calcium by permitting more calcium sulphate to enter solution. The calcium ions increase beyond their limit of saturation and tend to unite with the carbonate radical. The calcium carbonate is deposited on sand grains forming oolite or upon masses of algae, principally *Aphanothece* and *Microcystis*, forming a tufa-like deposit. In the latter case algae accumulate in shallow water and become cemented down to the increasing bed of tufaceous deposit. This is particularly evident along the shores of the islands and the promontory. Another type of deposit composed of a combination of oolite and tufaceous accumulations is evident in many places. Masses of algae together with the empty nymph shells of the salt fly are washed up on the shore and become incorporated with the grains of oolite. Repeated washing by the waves leaves more and more calcium carbonate in this heterogeneous mass. In this condition the algae become partially disintegrated, forming a mushy mass 4–6 inches deep, the color varying from the naturally bluish green and brown to light tints of pink, yellow, and hyaline. Acres of this gelatinous material are common along the eastern shore. As the lake recedes this material is left exposed on the beach and gradually dries out, resulting in the formation of crusty biscuit-like deposits 1–2 inches thick and 1–3 feet in diameter. These masses are built upon one another and become covered with wind-blown oolite. In time they are transformed into a friable platelike rock resembling

disintegrating sandstone. Older deposits show a thin undulated tufaceous rock, white to pale yellow in color and weathering into small plates. Hardpan and other calcareous deposits have been found in Jordan Valley a few inches to 10 feet deep and 5–10 miles from the present shore of the lake, indicating that this process of rock formation has been taking place over an extended period of time. Along the eastern shore, from the Jordan delta to the mouth of the Weber River, silt together with the vegetable matter becomes incorporated with the algal masses and is turned black by the action of sodium carbonate. As the lake recedes it is left exposed, the surface variegated and apparently solid, but really soft and gelatinous, 6–10 inches deep, and jet black. As the hot sun plays upon it, it puffs up and emits gases of strong sulphurous briny odor. The crusty formations are much the same as those just described, except that they are black with a hoary coat of salt.

While the flora of the lake waters is very limited in number of species of algae, it exerts an important influence on the shore deposits and is directly instrumental in the formation of a specific type of substratum upon which other plants encroach. The ecological significance of the algae becomes two-fold, first, as inhabitants of one of the most highly concentrated natural brines, and, second, as the agents of deposition.

Strand

The term "strand" as used in this paper includes any ground left exposed between the margin of the water and the highest level attained by the lake since records have been kept. This level is well defined by the old shore of 1868. The lateral extent may vary from a few feet near the headlands to nearly 2 miles on the flat beaches. The bars between the mainland and Antelope and Stansbury islands are often exposed. Seasonal variations alter the strand greatly.

The strand deposits may be divided into three groups: sand, oolitic limestone, and mud. The usual conditions show a laminated character of alternating layers of gray, black, and greenish black sediments. The coloring is due to the decay of algae and finely divided vegetable matter brought in by the rivers. Mud and silts occur mainly near the inlets and river deltas. Within a given area the fineness and uniformity of sand and mud may be continuous over a

rather extended range. Where hardpan is in process of genesis a coarser element is introduced.

FLORA.—For the most part the strand is barren. Trees are absent and shrubby plants rare. The pioneer vascular plants are restricted to the extreme margins and occasionally are scattered in isolated groups on the salt flats. The principal types invading the highly concentrated alkali soils may be considered briefly.

The samphires, *Salicornia rubra* and *S. utahensis*, are the first pioneer types of the halosere of Great Salt Lake. They tolerate a higher percentage of alkali in the soil than do any other species. *S. rubra* is an annual plant with opposite branches and minute scale leaves. It is a singular feature that the higher the salt content becomes the shorter and more densely crowded these plants grow. At the very margin of invasion stands 2 inches high are so dense that it would seem impossible for another plant to enter among them. In some places it may be seen to cover a strip of outer strand 30 feet wide, and again it may be absent. In mildly saline soil it reaches a maximum height of 12–14 inches. *S. utahensis* is an endemic plant, perennial, and more robust than the red species. It forms dense caespitose colonies and develops little hummocks of wind-blown material.

Second only to the samphires in toleration of alkali and in its habit of invading is the pickleweed, *Allenrolfea occidentalis*. It is a perennial which becomes shrubby at the base. The stems and leaves are much like those of the samphires but are characterized by alternate branching, and the plant as a whole is much larger and with a different habit of growth. It is common in certain parts of the strand region, invading barren flats, building up little hummocks of wind-blown sand and dust. The annual inkweed, *Suaeda erecta*, is another plant prominent in invasion of the strand. It is less tolerant of alkali and generally follows the samphires and pickleweed. A perennial species, *S. moquinii*, is of more robust habit and often follows the former species. The salt grass, *Distichlis spicata*, is perhaps the most versatile plant in the region. It usually follows the preceding species in the succession, but also enters the strand directly, sending out long rootstocks with the individuals arranged in straight lines.

Less common is *Atriplex hastata*. It is also very versatile though

never attaining any degree of dominance. In soils bearing a moderate amount of alkali and which are dry it is rather small, slender, and silvery gray in color. In very moist or wet soils it becomes tall, branched, and with dark green fleshy leaves. The two types were once regarded as separate species. *Scirpus americanus* and *S. paludosus* are swamp plants tolerant of alkali. They enter the strand at fresh-water inlets, bays, and deltas where the strong alkali is somewhat reduced.

While halophytes become smaller in size the more highly concentrated the salt becomes, the opposite extreme is noted in less saline situations where they reach a maximum size. If, however, the alkali content of the soil becomes less than the optimum, the plants become smaller and more spindling. This situation is seldom observed in nature since competition with other plants soon eliminates them. An example of this is noted in river deltas where the rushes eliminate the samphires.

A point of particular interest is the water relationship of these plants. While the data may tell the percentage salt in soil samples when dry, they tell little regarding the actual conditions while the plants are growing in them. This is due mainly to the varying amounts of water. It has been noted that samphires grow in soils bearing as high as 6.5% salt, calculated from the dry weight of the soil. It is important to note, however, that such soils as harbor samphires have a relatively high water content and that the real feature of significance is the concentration of the soil solution. In the spring the water table is high and the sands and clays are saturated, the concentration is reduced, and germination and growth are initiated. Once started, and the plants having become established, subsequent withdrawal of the water is common. The reaction of the plants differs according to the amount of salt present and the type of soil. Plants persist longer in dry sandy soil than they do in dry clay. The rapidity with which the soil is dried is also a condition bringing about variable plant reactions. In both sandy soil and clay, the slower the drying process the more tenaciously the plants persist, even after the soil becomes very dry and cracked. If the soils are dried out rapidly, however, the plants perish even while there is ample water available.

Several samples of soil were taken from the root region of various typical halophytes and analyses made for water content, total salts, and in some instances for basic constituents. The salts were extracted with excess distilled water, the liquid passed through a porcelain filter, and the filtrate used in standard quantities for analyses. The H-ion concentration was determined with indicator solutions. Typical transects were selected and soil samples taken from the various successional zones. From a number of transects two series of results

TABLE VI

CHEMICAL ANALYSES OF SOILS FROM LITTLE MOUNTAIN AREA; SALTS CALCULATED ON BASIS OF DRY WEIGHT OF SAMPLES. COLLECTED JULY 20, 1929. THE FIRST THREE WERE SAND, THE REMAINDER CLAY

LOCATION	WATER CONTENT	pH	NaCl	Na_2CO_3	$NaHCO_3$	Na_2SO_4	TOTAL
Barren salt flat 25 feet from plants	20.84	8.9	17.68	0.339	Trace	4.572	22.59
Two feet from first Salicornia plants	15.94	8.8	5.89	0.005	0.05	0.852	6.72
Salicornia rubra pioneers	15.81	8.8	5.30	0.005	0.05	0.401	6.26
Suaeda erecta zone	14.80	9.8	2.60	0.005	0.672	Trace	3.31
Distichlis zone	8.22	8.8	2.21	0.053	0.141	Trace	2.60
Cressa depressa zone	8.2	9.0	0.651	0.005	0.605	Trace	1.30

are presented here, illustrating the extreme alkali conditions and the average conditions respectively.

LITTLE MOUNTAIN AREA.—The strand at this point shows remarkable plant zonation, although the type of soil changes abruptly. The outer margin toward the lake is black sand and harbors pioneer samphires and a few annual inkweeds. The soil then changes to a heavy clay which bakes hard in late summer. In this part the inkweeds and salt grass are abundant, with scattered *Atriplex hastata*. Farther removed is a zone of *Cressa depressa* and some patches of *Sida hederacea*. *Salicornia rubra* at the margin of invasion is very short and becomes larger as the salt content of the soil decreases. Table VI shows the water, salt content, and pH of the soil.

The high salt content in these zones shows a unique extreme in salt tolerance and was the highest found in the region. KEARNEY,

BRIGGS, and SHANTZ (7) carried on investigations in Tooele Valley and report the average salt content of the *Salicornia* zone at 2.5%. HALKET (6) demonstrated that some species of *Salicornia* tolerate salt up to 5% in artificial cultures. The strand at this point has a high water table and the soils are saturated until summer sets in and then they begin to dry out slowly. The abundant water serves to dilute the strong salt and may be the main factor permitting the plants to survive in this highly saline habitat.

EASTERN SECTION.—The relatively flat beaches are of fine gray sand for the most part, with local areas of coarse calcareous material and decaying algal masses. Invading plants form an irregular line toward the lake side and seem to be limited only by high salt content of the soil and to a less extent by the mucky algal masses. The samphires are the most frequent plants to enter the barren areas, although the annual inkweed and salt grass lead the invasion in many places. Several transects of soil samples were taken through typical situations and the water and alkali conditions studied. The results bear out the conclusion that the critical period determining the vegetation is early spring when the water table is high and the strong soil solutes are more dilute than later in the season. The optimum salt concentration for the samphires ranges between 2.5 and 3.5% during the early spring, but conditions become variable as the water withdraws. Table VII shows the analyses of a typical area taken in July after the water table had gone down considerably.

The H-ion concentration of the soils throughout the region seems to show little or no relationship to the types of vegetation and in no way was it possible to use this as a factor determining the species or vegetation.

FLORISTICS.—The floristic features may be divided according to the predominating soil and topographic features, and in addition, the climatic and surface water relations. The eastern section receives about 10 inches more rainfall than the northern and western portions.

The eastern section, extending from Little Mountain to the Jordan delta, presents a strand of diverse situations. Numerous strand swamps, inlets, and springs introduce contrasting plant communities, while the greatest extent of the strand shows the usual pioneers al-

ready cited. The soil is of the black sand type previously mentioned. A bluff or terrace has been cut in the old delta deposits of the Weber River so that there is an abrupt break in the vegetation. This topographic feature narrows the successional zones so that there are no gradual transitional zones between the pioneer and intermediate types. To the north and south the terrace dwindles and the extremities show the gradual entrance of species from the saline plains.

The section extending from the Jordan delta to the southern tip of the lake is likewise one of diversity, with strand swamps, springs, calcareous dunes, and rocky headlands. The flora in this section

TABLE VII

ANALYSES OF SOIL SAMPLES FROM SALTAIR AREA; SALTS CALCULATED TO DRY WEIGHT OF SOIL. COLLECTED JULY 12, 1929

LOCATION	WATER CONTENT	pH	NaCl	Na_2CO_3	$NaHCO_3$	Na_2SO_4	TOTAL
Invading Salicornia rubra.....	14.10	8.4	4.08	0.052	0.022	0.853	4.99
Suaeda erecta zone surface soil....	9.14	8.8	2.68	0.084	Trace	1.421	4.80
Same, 2 feet deep.	18.20	8.4	1.51	0.084	Trace	0.433	2.01
Distichlis zone surface soil....	3.59	8.6	0.07	0.057	Trace	0.497	0.62
Same, 2 feet deep.	10.81	8.6	0.06	0.10	0.012	0.384	0.54

sums up suitably most of the features common to the entire eastern side of the lake. The sand is very fine along the water's edge but toward the outer margin it becomes coarser, with calcareous material predominating. The invading species grow mainly in this coarser soil but a few may be noted in isolated colonies on the sand flats.

Generally there are several well defined zones. The pioneer types are more or less constant but the zones further removed become more and more diverse. This becomes evident in passing from one situation to another; the same pioneers persist but those following change or form different combinations with other species. Notable among the sandy beach elements are *Spartina*, *Abronia*, *Eriocoma*, and *Sphaerostigma*. The succession on the Saltair and Garfield beaches shows the following zones:

Zone 1. Salicornia rubra A. Nels.
S. utahensis Tidest.

Zone 2. Suaeda erecta (Wats.) A. Nels.
Zone 3. Distichlis spicata (L.) Greene
Zone 4. Spartina gracilis Trin.
Eriocoma cuspidata Nutt.
Puccinellia nuttalliana (Schultes) Hitchc.
Bromus tectorum L.
Abronia salsa Rydb.
Sphaerostigma utahensis Small
Zone 5. Sporobolus asperifolius (Nees. & Mey.) Thurb.
Distichlis spicata (L.) Greene
Atriplex hastata L.

Zones 4 and 5 are the most variable. Frequently *Suaeda moquinii* is present. The following plants are also common entrants:

Sporobolus airoides Torr.
S. cryptandrus (Torr.) Gray
Poa nevadensis Vasey
Bromus tectorum L.
Sitanion hystrix (Nutt.) J. G. Smith
Atriplex hastata L.
A. confertifolia (Torr.) Wats.
A. rosea L.
Pachylophus marginatus (Nutt.) Rydb.
Gutierrezia microcephala Gray
Chrysothamnus pulcherrimus Greene
Iva axillaris Pursh

Most of these plants are common inhabitants of the calcareous dunes forming the outer limits of the strand.

BURMISTER-DELLE CREEK SECTION.—This section is at the southern extremity of the lake and presents one of the broadest stretches of exposed beaches. At times when the lake is low the Stansbury Bar is exposed throughout the year, and only during the spring months are the extensive flats saturated with water. This is mainly precipitation and ground water. The general aspect presents a barren salt flat, white on the surface but with the underlying strata yellowish and with gray clays laminated with darker streaks. It retains the water until late summer when the outer margins become dry and cracked.

The topography north of Burmister and on the Stansbury Bar is interesting, as the salt flats are interrupted by a number of small island-like raised areas which stand 4–6 feet above the general level. They are composed of clay loam and harbor a flora of greasewood and shadscale which extends to the very margin and produces a marked contrast with the barren salt flats. These islands vary in size up to several hundred yards across.

For the most part there is no vegetation on the flats. Toward the mainland a few outposts of *Allenrolfea* and occasionally *Salicornia* appear in scattered colonies. *Allenrolfea* is almost the exclusive pioneer plant in many places. It builds the little hummocks described previously, often giving the surface a spotted appearance. The salt grass is generally the next plant to enter, with its characteristic habit of sending out long root stocks. A variety of plants may enter next, depending upon the locality and the conditions. The eastern portion finds a rich development of *Salicornia utahensis*, especially along moist playas where springs occur. Most of the portions surrounding the islands have species of *Suaeda* entering next, while toward the western portion little playa meadows are common. These may be occupied almost exclusively by salt grass or a mixed flora of salt grass, *Sporobolus airoides*, *S. cryptandrus*, *Puccinellia nuttalliana*, *Triglochin maritima*, and *Cressa erecta*.

The succession is various, often narrow in its zonation, and difficult to follow. The following arrangement indicates the usual order of approach:

Zone 1. Allenrolfea occidentalis (Wats.) Kuntze
Suaeda erecta (Wats.) A. Nels.
S. moquinii (Torr.) A. Nels.
Zone 3. Distichlis spicata (L.) Greene
Zone 4. Suaeda diffusa Wats.
Atriplex confertifolia (Torr.) Wats.
Sarcobatus vermiculatus (Hook.) Torr.

STANSBURY ISLAND.—The strand of Stansbury Island is continuous with that of the mainland at the present time. On either side at the south end it is very broad but it becomes gradually narrowed toward the middle of the island. On the east side and at the north it is

narrow, and often steep and rocky. In general the flora is much the same as that already described. The main contrasting feature is the presence of two parallel beach bars along the eastern shore near the middle. They are composed of a coarse, clean white calcareous sand arising from a shore of friable hardpan in process of genesis. The vegetation is in distinct zones with a number of new entrants. Notable among the latter are *Mentzelia, Cleome,* and *Amelanchier mormonica*. The steep slopes immediately behind these bars make it possible for a number of non-halophytic plants to make a rather close approach to the lake. The following zones may be recognized:

Zone 1. Salicornia rubra A. Nels.
S. utahensis Tidest.
Zone 2. Suaeda erecta (Wats.) A. Nels.
Allenrolfea occidentalis (Wats.) Kuntze
Zone 3. Atriplex argentea Nutt.
Amaranthus graecizans L.
Salsola pestifer A. Nels.
Mentzelia laevicaulis (Dougl.) T. & G.
Sphaerostigma utahensis Small
Zone 4. Distichlis spicata (L.) Greene
Bromus tectorum L.
Cleome serrulata Pursh
Amelanchier mormonica C.K. Schneider

In this vicinity a number of dead stumps of *Sarcobatus* and *Tetradymia spinosa* were observed, suggesting that the succession at one time reached a somewhat advanced stage before the rise of the lake killed them. In some places there is a well defined line of empty shells of the salt fly larvae, indicating the upper limits of the storm waves.

Western and Northern sections.—The broadest expanse of barren strand is to be found in the western and northern portions of the lake. In many places the water's edge is nearly 2 miles from the old shore line. The white salt flats are interrupted only by drift wood and occasional hummocks of *Allenrolfea*. The latter were found nearly a mile out on the flats, with no intervening vegetation. In the major features the plants merely accentuate the richness and

halophytic character of the vegetation. The species show no further features beyond those already considered, and only local variations distinguish the region from the successional zones of the eastern and southern sections. The topography presents a very irregular line marking the old shore; long narrow terraces extend toward the lake with deep sinuous bays separating them. In the latter, salt grass meadows are common while pure strands of the various species may be found. Rich growths of *Suaeda*, *Salicornia*, *Allenrolfea*, and the several species of *Sporobolus* show these plants at their best.

The main influences of climate lie in light, heat, and evaporation. The bright glaring sunlight is perhaps more apparent than real and does not compare with that of high mountain tops, but the vegetation receives a maximum amount for valley regions. The surface temperature of the soil often reaches 36° to 38° C. The evaporation is high, and although the water supply is ample during the spring and early summer months, the gradual withdrawal of the ground-water, together with the increasing concentration of the soil solution, renders the strand one of the most unique of ecological situations.

Inlets, strand swamps, and springs

Fresh-water inlets and springs are common along the eastern side of the lake. At their points of entry into the lake the concentration of the salt is greatly reduced and a number of contrasting situations are to be found.

Bear River Bay.—The northern and eastern portions of Bear River Bay are bordered by broad mud flats, while the western border is more abrupt with several rocky points and numerous mineral springs on the strand. The Southern Pacific Railroad trestle extends across the mouth of the bay and forms a barrier which tends to retain the fresh-water in the bay and exclude the strong brines from the main body of the lake. The reduction in amount of salt from the trestle northward is as follows:

Little Mountain just north of the Southern Pacific trestle	18.01%
Willard Spur, south side	11.68%
Willard Spur, north side	8.60%

WILLARD SPUR AREA.—The Willard Spur is a shallow arm of Bear River Bay which extends eastward. The mud flats and substratum of the shallow water are undulating, with numerous slight depressions which retain little pools as the water recedes. Flaky accumulations of decaying vegetable matter lie half suspended in the water, while countless small crustaceans (*Cypris* sp.) crowd the margins and are left stranded as the water recedes. In the shallow pools a form of *Cladophora fraeta* occurs, often becoming very abundant. *Potamogeton pectinatus* and *Ruppia maritima* are other

TABLE VIII

PERCENTAGE MOISTURE, pH, AND PERCENTAGE TOTAL SALTS OF SOILS FROM WILLARD SPUR (SALTS ON BASIS OF DRY WEIGHT OF SAMPLES). COLLECTED JUNE 29, 1929

LOCATION	WATER CONTENT	pH	TOTAL SALTS
Clay silt from bottom of shallow pool	31.6	8.4	2.01
Clay flat, 20 feet from water	22.0	8.4	1.83
Dry clay flat, Salicornia wilting	10.2	8.6	1.76
Clay cracked and dry, Salicornia dead	8.0	8.8	1.31
Clay loam bordering cultivated fields	21.7	8.6	1.35
Same with Suaeda erecta	14.0	8.6	0.91

members of the aquatic society. *Salicornia rubra* germinates and reaches a robust size in water 2–3 inches deep. On the mud flats it is abundant as long as the water remains, but as summer passes desiccation becomes more and more severe until there is no longer sufficient water to maintain vegetation. The plants follow the water as it recedes. A transect of soil samples was taken from the water's margin for a mile back to the old shore line. Table VIII shows the analyses.

Lack of circulation of the water in the shallow portions of bays permits the accumulation of heat. Thus on July 29, with the air temperature at 32° C., the water of the main body of the lake was 19° C. at midday while the shallow water of Willard Spur was 31° C.

The mud flats are inhabited almost exclusively by *Salicornia rubra*. Following are a few scattered *Allenrolfea*, then an irregular zone of *Atriplex hastata*, and next an irregular zone of *A. truncata*. Grasses

enter next with numerous annuals and a few shrubs, forming a mixed association as follows:

Hordeum jubatum L.
H. gussonianum Parl.
Polygonum aviculare L.
Sarcobatus vermiculatus (Hook.) Torr.
Lepidium perfoliatum L.
L. pubicarpum A. Nels.
Sisymbrium altissimum L.
Allocarya nitens Greene
Matricaria suaveolens (Pursh) Buchen.
Grindelia squarrosa (Pursh) Dunal
Helianthus annuus L.

In seepage areas the following appear:

Puccinellia nuttalliana (Schultes) Hitchc.
Hordeum jubatum L.
Atriplex hastata L.
Spergularia salina Presl.
Ranunculus eremogenes Greene
Halerpestes cymbalaria (Pursh) Greene

THE PROMONTORY.—The strand on the east side of the Promontory is narrow, the mountains rising rather abruptly from the shore. A few steep headlands are conjunctive with the strand and the beach is strewn with rocks, in some places forming a shingle beach. The residual rocks are near the surface and numerous springs arise through the crevices, some bearing minerals and flammable gases.

The following algae were recorded:

Oscillatoria animalis Ag.
O. spp.
Enteromorpha intestinalis L.
Vaucheria sp.
Spirogyra sp.

The steepness of the strand in many places makes the zones of transition between the strongly saline soils and fresh soils very narrow, and consequently the successional zones are much contracted

and overlapped. The following zones are generalized from several situations:

Zone 1. Salicornia rubra A. Nels.
Zone 2. Polypogon monspeliensis (L.) Desv.
Distichlis spicata (L.) Greene
Zone 3. Hordeum jubatum L.
Halerpestes cymbalaria (Pursh) Greene
Zone 4. Scirpus americanus Pers.
S. paludosus A. Nels.
S. olneyi Gray

Meadows and muddy banks show a variety of plants and three main groups may be identified according to the degree of halophytism. Where the salt is strong the following occur:

Puccinellia nuttalliana (Schultes) Hitchc.
Distichlis spicata (L). Greene
Polypogon monspeliensis (L.) Desv.
Hordeum jubatum L.
H. gussonianum Parl.
Sitanion sp.
Juncus balticus Willd.
Rumex crispus L.
Suaeda erecta (Wats.) A. Nels.
Atriplex rosea L.
A. argentea Nutt.
A. hastata L.

Other situations show many composites:

Triglochin maritima L.
Sporobolus airoides Torr.
Spergularia salina Presl.
Melilotus alba Desv.
Achillea millefolium L.
Aplopappus lanceolatus (Hook.) T. & G.
Agoseris spp.
Helianthus annuus L.
Iva axillaris Pursh
Leontodon taraxacum L.

Some seepage areas have leached much of the alkali from the soil and present the following:

Lemna minor L.
Carex sp.
Berula erecta (Huds.) Coville
Glaux maritima L.
Asclepias speciosa Torr.
Castilleja exilis A. Nels.
Sonchus asper (L.) Hill

On the upper dry side of some of these mildly saline situations *Cleome serrulata* grows in dense masses; *Euphorbia glyptosperma*, *Polygonum aviculare*, *Artemisia tridentata*, and several species of *Chrysothamnus* are also found.

EASTERN SECTION.—From Little Mountain to East Bay there are numerous inlets and strand swamps. They are much alike in character and composition with a few variations according to the situation. *Cladophora* and *Spirogyra* are common; *Scirpus americanus* and *S. paludosus* usually appear in the inlets; the grasses *Puccinellia*, *Hordeum jubatum*, *Polypogon*, and *Distichlis* are common. Near the village of Hooper is a shallow strand swamp harboring a low and rather uniform vegetation. It is characterized by many small water channels with tussocks of plants and decaying accumulations. The algae are abundant; *Potamogeton pectinatus* and *Ruppia maritima* are submerged types and *Lemna minor* floats on the surface. The emergent society is composed of:

Sagittaria cuneata Scheld.
Scirpus spp.
Eleocharis palustris (L.) H. & B.
E. acicularis (L.) R. & S.
Cicuta occidentalis Greene
Berula erecta (Huds.) Coville

On the borders and on heaps of decaying vegetable matter the following enter:

Polypogon monspeliensis (L.) Desv.
Puccinellia nuttalliana (Schultes) Hitchc.
Sporobolus airoides Torr.

Atriplex hastata L.
Trifolium pratense L.
Epilobium adenocaulon Hausskn.

The swamp community in East Bay is one of contrasts. The outer portion toward the lake is much more saline than the portion toward the shore. The salt content of the water was found to be 5.86 and 1.03% respectively. The algae are abundant, appearing at a distance like a green meadow. *Salicornia rubra* is prominent and grows in water 2 or 3 inches deep. *Scirpus* spp. are present while *Typha* enters as a new member. The associated species include those already mentioned and also *Scirpus lacustris*, *Ranunculus eremogenes*, *Halerpestes cymbalaria*, and *Radicula nasturtium-aquaticum*.

Numerous other strand situations occur in other sections surrounding the lake, but present only slight variations of those cited. Black Rock, Lake Point, Delle Creek, and near the Salt Wells are other localities where fresh water enters.

River deltas

As physiographic units the deltas of the three largest rivers tributary to the lake are much the same in the character of the sediments deposited and in their vegetation. All are composed of heavy dark brown or gray clays of varying alkali content. The rivers are muddy. At present the conditions are much altered by the interference of duck clubs, dikes having been built around the distal extremities of the Jordan delta and across the north limb of the Bear River delta. Headgates in the dikes are closed during part of the year and the water backed up in the delta, extending the marsh land. Headgates have also been built at the point where the rivers enter the deltas and the flow of water through the various channels regulated. In the Jordan delta 3600 acres are submerged to a depth of 3 feet. Every spring the headgates are opened and the deltas drained. Strong winds often blow the lake brine back into the deltas, killing numerous fish and other animals besides increasing the alkali content of the soils.

The soil and water conditions when the Jordan delta was drained are shown in table IX.

The vegetation is augmented by introduction of seeds and cuttings of plants beneficial to ducks and other birds. Among the plants introduced are:

Sparganium eurycarpum Engelm.
Potamogeton pectinatus L.
Ruppia maritima L.
Scirpus americanus Pers.
S. validus Vahl.
S. lacustris L.
S. paludosus A. Nels.
Puccinellia nuttalliana (Schultes) Hitchc.

The seeds of these plants are relished very much by birds, and extensive fields of *Scirpus americanus* are cultivated. When the

TABLE IX

CHEMICAL ANALYSIS OF SOILS FROM JORDAN DELTA; SALTS CALCULATED IN TERMS OF DRY WEIGHT OF SAMPLES. COLLECTED JULY 29, 1929

LOCATION	WATER CONTENT	pH	NaCl	Na_2CO_3	$NaHCO_3$	Na_2SO_4	TOTAL SALTS
Salicornia.....	26.8	8.6	0.323	0.084	Trace	1.56	2.08
Scirpus spp.....	22.8	8.6	0.389	0.084	"	0.99	1.40
Typha and Sparganium.....	25.8	8.6	0.328	0.082	"	0.81	1.27

deltas are drained in the spring the mud flats dry out and by August the fields are mowed. The following societies constitute the dominant flora:

Free-floating:

Spirogyra sp.
Cladophora fraeta forma

Anchored submerged:

Potamogeton pectinatus L.
Ruppia maritima L.

Emergent types:

Scirpus americanus Pers.
S. paludosus A. Nels.

S. lacustris L.
S. validus Vahl.
S. olneyi Gray

Emergent types restricted to muddy banks:

Sparganium eurycarpum Engelm.
Typha latifolia L.
T. angustifolia L.
Phragmites communis Trin.
Puccinellia nuttalliana (Schultes) Hitchc.
Distichlis spicata (L.) Greene
Rumex crispus L.
R. britannica L.
Salicornia rubra A. Nels.
Sonchus asper (L.) Hill

Types restricted to banks:

Triglochin maritima L.
Spartina gracilis Trin.
Hordeum jubatum L.
Polypogon monspeliensis (L.) Desv.
Atriplex hastata L.
A. rosea L.
Suaeda erecta (Wats.) A. Nels.
S. moquinii (Torr.) A. Nels.
Amaranthus retroflexus L.
Sida hederacea (Dougl.) Torr.
Asclepias speciosa Torr.
A. mexicana Cav.
Apocynum cannabinum L.
Iva axillaris Pursh
I. xanthifolia Nutt.
Grindelia squarrosa (Pursh) Dunal
Xanthium pennsylvanicum Wallr.
Helenium autumnale L.
Lactuca scariola L.
L. integrata (Gren. & Godr.) A. Nels.

Halerpestes cymbalaria becomes prominent along the margins after the delta is drained, while *Salicornia* invades the barren flats.

Playas and alkaline plains

A large part of the valleys surrounding Great Salt Lake have soils that are strongly alkaline. Successively these valleys have been the bed of the lake and the strands, and at present they have been reclaimed to a large extent by vegetation. The general physiographic features show a plain interrupted by playas, sloughs, drainage canals, and streams. Permanent streams traverse the region mainly on the eastern side, and it is on this side that much of the land has been turned to agricultural uses wherever drainage has been possible.

SOIL, ALKALI, AND GROUND-WATER.—Coarse grained oolitic sands and hardpan derivatives are common along the lake borders. The surface soil of the plains is dominantly Jordan loam with a subsoil of loam or clay. In the depressions the surface soil is usually Jordan clay with a subsoil of the same character. Sand is not frequent and hardpan is a subsoil type.

In a given column of soil the alkali content is often governed by the amount of water in it. In regions where the water table is deep the precipitation water tends to carry the salt deeper into the soil, leaving the surface layers with relatively small amounts. On the other hand, where the water table is close to the surface the water is drawn to the surface, carrying with it the soluble salts which are deposited in the upper layers of soil. A number of surveys of the soil and water conditions (**1, 5, 7, 10, 11**) furnish data which show that the percentage of alkali in the soil increases roughly in proportion to the shallowness of the water table, as follows:

Depth of water table below surface	Percentage of alkali
3 feet or less	3% or more
6 feet	1–3%
10 feet	0.25–1%

Specific data correlated with the vegetation will be given in the following sections.

Playas

Playas are numerous and occur in nearly all parts of the valleys. Generally they are alike in soil, alkali, and water relations, few showing marked differences from the general conditions exhibited by the majority. Floristically they are strikingly similar although local variations are common. A distinction must be drawn for a correct understanding of this presentation. For convenience they may be considered in three groups: (1) the young undeveloped situations usually presenting a barren flat with a pioneer vegetation encroach-

TABLE X

GENERALIZED SOIL TRANSECT OF PIONEER PLAYA SHOWING PERCENTAGE ALKALI CALCULATED IN TERMS OF DRY WEIGHT OF SOIL. WATER TABLE THREE FEET OR LESS IN EACH INSTANCE. JUNE 25, 1929

No.	Type of plant	Surface	2 feet	3 feet
41	Barren area	7.06	6.55	10.91
42	" "	3.55	6.60	5.30
43	" "	3.02	5.05	5.00
54	Salicornia rubra	2.42	.....	.....
44	" "	2.00	4.15	4.11
35	Allenrolfea	0.98	1.00	1.03
36	"	1.54	1.61	1.60
45	Suaeda erecta	1.47	2.03	1.98
46	" "	1.48	1.68	1.70

ing from the margins; (2) the intermediate situations where the entire playa has been invaded; (3) those which have been reclaimed by a halophytic flora. Most playas are alike in the early stages but diverse in the intermediate stages. None was observed in the mature stage.

Pioneer stages.—Pioneer types of the playas are much the same as those of the strand. The main difference lies in the habit and distribution of the plants. *Salicornia rubra* and *S. utahensis* are the most frequent species invading the barren playas, although *Allenrolfea occidentalis*, *Suaeda erecta*, *S. moquinii*, *S. occidentalis*, and *Distichlis spicata* are not uncommon in this capacity also. There seems to be little reaction of the plants to the type of soil in which they grow. The great determinative factor is a certain amount of

water; the great unifying factor is a certain amount of alkali. The amount of salt present in dry soils varies greatly, ranging from 0.05 to 10.0%. The concentration of soil solute depends upon the amount

TABLE XI

DOMINANT HALOPHYTES AND THEIR pH RELATIONS

No.	Type of plant	Locality	Type of soil	pH
109	Barren	Jordan Valley	Jordan clay	8.0
112		" "	" "	8.6
138		Weber Valley	" "	8.9
139	Salicornia	Weber Valley	Salt Lake sand	9.0
108		Jordan Valley	Jordan loam	8.6
115		" "	" "	8.7
121		" "	Salt Lake sand	8.4
169		Tooele Valley	Hardpan	8.4
170		" "	Jordan clay	8.5
110	Suaeda erecta	Jordan Valley	Jordan clay	8.6
125		" "	Salt Lake sand	8.4
186		" "	Jordan loam	8.4
151		Weber Valley	Salt Lake sand	9.8
140		" "	" " "	9.8
125	Suaeda moquinii	Jordan Valley	Salt Lake sand	8.4
132		" "	Jordan loam	8.6
152		Weber Valley	Salt Lake sand	9.8
106	Allenrolfea	Jordan Valley	Jordan clay	9.0
110		" "	" "	8.6
111		" "	" "	8.2
187		" "	Jordan loam	8.5
189		" "	" "	8.6
145		Weber Valley	Jordan clay	8.6
146		" "	" "	9.0
159		Tooele Valley	" "	8.8
162		" "	" "	9.1
105	Distichlis	Jordan Valley	Jordan clay	8.8
181		" "	Salt Lake sand	9.1
185		" "	Jordan loam	8.4
193		" "	" "	8.6
200		Jordan delta	Jordan clay	8.6
153		Weber Valley	Salt Lake sand	9.6

of water in the soil, which is an extremely variable factor during the growing season. Soils of low percentage of salts and a small amount of water become as drastic as soils with high salt percentage and a large amount of water. Thus the strand has high percentage of salt and the water table is slow to withdraw, and *Salicornia* thrives in

these conditions. On the other hand the playas lose water faster and the soil solutes concentrate faster, so that the plants can persist only in soils showing approximately 2% salt in terms of dry weight. The values obtained from soil analyses of typical playa successions show the series to be very similar. The *Salicornia* belt averages about 2% salt, *Suaeda erecta* about 1.5%, and *Allenrolfea* about 1%. None of these plants was found in extremely strong salt as was the case on the strand. Table X represents the average conditions found in typical playas.

No correlation could be made between the H-ion concentration of the soil and the type of plants growing in it, nor could any correlation be made between the H-ion values and the types of soils and their water content. With such a range of values little can be interpreted other than the fact that these plants will tolerate a rather wide range. Table XI gives specific data in this connection.

INTERMEDIATE STAGES.—In the following discussions the term "intermediate stage" covers a number of diverse situations. In most playas there is generally an increase in the amount of alkali from the borders toward the center, so that the succession of plants follows as fast as the alkali is reduced. In some playas this is apparently not the case, however, but the alkali content is more or less uniform in all parts. In the first instance the vegetation is mixed and in the latter it is more or less homogeneous.

MIXED PLAYA SUCCESSION.—Following the pioneer species are two rather well defined belts of plants, the first group dominated by the Chenopodiaceae and the second by a number of small annuals. In group one the first three species named make up the vernal aspect and the remainder the summer aspect.

Triglochin maritima L.
Bromus tectorum L.
Puccinellia nuttalliana (Schultes) Hitchc.
Atriplex argentea L.
A. hastata L.
Suaeda intermedia Wats.
S. moquinii (Torr.) A. Nels.
Salsola pestifer A. Nels.

Bassia hyssopifolia (Parl.) Kuntze
Sesuvium sessile Pers.

The second group following these plants includes:

Deschampsia danthonioides Monro.
Myosurus apetalus Gay
Lepidium perfoliatum L.
L. dictyotum Gray
Hutchinsia procumbens (L.) Desv.
Arabis spp.
Allocarya nitens Greene
Plantago elongata Pursh
P. purshii Roem. & Schult.
Psilocarphus globiferus Nutt.

Of this second group all are annuals except *Deschampsia danthonioides*, and compose the vernal aspect. The alkali content of the soil of the first belt averages about 1.0% and of the second belt from 0.6 to 0.8%.

The terraces bordering the playas harbor a greasewood and shadscale association and certain elements of this association are creeping out on the playas. Among the plants noted are:

Atriplex confertifolia (Torr.) Wats.
A. nuttallii Wats.
Kochia vestita (Wats.) A. Nels.
Eurotia lanata (Pursh) Moq.
Sarcobatus vermiculatus (Hook.) Torr.
Tetradymia spinosa Gray

RECLAIMED HOMOGENEOUS PLAYAS.—It is assumed that a playa is reclaimed when it is occupied by plants in such numbers as to create sharp competition among them. In many instances a single species may invade a new area so as completely to occupy the ground and preclude the entrance of any other species except an occasional plant here and there. Uniform conditions partly explain this situation, but the more apparent reason is that the one species got there first in great numbers. Where playas are reclaimed by a single species there is usually a robust growth showing the plant at its optimum.

Soil samples were taken from selected communities of this type and the salt contents are shown in table XII.

SALICORNIA FLATS.—There are a few instances where a playa becomes completely invaded by dense growths of *Salicornia*. Usually in such areas the salt is rather strong but does not exceed the optimum of about 2.5 to 3%. The water table is usually high during a greater part of the year. One large community of this kind occurs in Hansel Valley.

TABLE XII

PERCENTAGE OF ALKALI IN SOILS OF RECLAIMED PLAYAS CALCULATED IN TERMS OF DRY WEIGHT. WATER TABLE 3 FEET OR LESS FROM SURFACE IN EACH INSTANCE. JUNE 28, 1929

No.	LOCALITY	SURFACE	2 FEET	3 FEET
32	Allenrolfea flat	1.41	1.12	1.16
35	" "	0.98	1.00	1.03
36	" "	1.54	1.61	1.60
34	Suaeda moquinii flat	0.81	0.80	0.74
25	" " "	1.03	0.95	0.99
31	Distichlis meadow	0.96	1.01	1.12
33	" "	0.96	1.45	1.22
34	" "	0.82	0.84	1.00
29	Sporobolus field	0.55	0.89	1.07
30	" "	0.54	0.83	0.97

ALLENROLFEA FLATS.—This plant prefers a more open distribution, and while it becomes dense several other species are scattered throughout the flat. The alkali optimum is from 1.0 to 1.4%. Hansel and Curlew valleys show numerous communities of this type. The commonest species occurring with it are *Salicornia rubra* and *Suaeda erecta*. *Distichlis* also occurs with it where the water table is high. Generally the pickleweed tends to stay more or less by itself.

SALT GRASS MEADOWS.—It is not unusual to see continuous areas of dense salt grass. Of all the halophytic species in this region it is the most cosmopolitan. It occurs in nearly every kind of situation that furnishes a fair supply of water during the spring and early summer months. As a competitor in successions it tends to eliminate most plants, and once established it is slow to yield to other vegetation. Its success lies mainly in its habit of sending out long root stocks with numerous individuals disposed in straight lines. Its range of alkali tolerance is perhaps wider than that of any other

species. It grows in mildly saline soil and will also enter the most drastic soils following the samphires. With its relatively high competitive power it will dominate the ground wherever it can.

Where salt grass is dominant there are few and usually scattered associates. The most frequent ones are *Allenrolfea*, *Atriplex*, and *Suaeda*. The following is a complete list:

Atriplex hastata L.
A. argentea L.
Suaeda intermedia Wats.
S. occidentalis (Wats.) A. Nels.
Sida hederacea (Dougl.) Torr.
Glaux maritima L.
Cressa erecta Rydb.
C. depressa Good.
Adenostegia ramosa (Nutt.) Greene

The seasonal aspect is almost entirely summer and fall.

SPOROBOLUS FIELDS.—*S. airoides* grows in coarse caespitose bunches where the alkali content of the soil is about 0.5%. It is noted as a ground-water feeder. Associated with it are *S. cryptandrus*, *S. asperifolius*, and *Bromus tectorum*, besides a great many other less common plants. While its sociability is marked its habit of growth and soil relations are such that it does not afford a great deal of competition. The coverage is rather uniform where it is dominant, presenting dense tufts of feathery character but usually rather widely disposed. Interspersed is a wide variety of species. Of all the reclaimed playa situations the *Sporobolus* fields are the most variable and represent the commonest type preceding the greasewood-shadscale association.

With the exception of the species of *Sporobolus* and *Sitanion*, most of the vernal flora is composed of annuals included in the Gramineae and Cruciferae. The composition is as follows:

Dominant species:

Sporobolus airoides Torr.
S. cryptandrus (Torr.) Gray
S. asperifolius (Nees. & Mey.) Thurb.
Bromus tectorum L.

Less common species:

Bromus hordeaceus L.
Hordeum gussonianum Parl.
Sitanion hystrix (Nutt.) J. G. Smith
Lepidium perfoliatum L.
L. dictyotum Gray
Malcolmia africana (Willd.) A. Br.
Draba nemorosa L.
D. micrantha Nutt.
Sophia pinnata (Walt.) Brit.
S. sophia L.
Sisymbrium altissimum L.
Camelina microcarpa Andrz.

In certain advanced stages in the reclamation of playas the vernal flora is followed by summer and autumn aspects represented almost exclusively by the Chenopodiaceae and Compositae. Notable among these are species of *Atriplex* and *Chrysothamnus*. The following is a more complete list, all of which are perennials:

Atriplex confertifolia (Torr.) Wats.
A. truncata (Torr.) Gray
A. nuttallii Wats.
Eurotia lanata (Pursh) Moq.
Kochia americana Wats.
K. vestita (Wats.) A. Nels.
Sarcobatus vermiculatus (Hook.) Torr.
Suaeda depressa (Pursh) Wats.
S. intermedia Wats.
S. moquinii (Torr.) A. Nels.
Gutierrezia microcephala Gray
Chrysothamnus nauseosus (Pall.) Brit.
C. pulcherrimus Greene
C. pinifolius Greene
C. viscidiflorus tortifolius (Gray) Greene
Viguiera ciliata (Robins. & Greene) Blake
Artemisia spinescens Eat.
A. tridentata Nutt.

GREAT AMERICAN DESERT.—This is a large playa 50 by 100 miles in extent and was the last extensive basin vacated by Great Salt Lake in its decline. The saline constituents permeate the soils to considerable depth and in many places the salt is relatively pure. The surface for the greatest extent is white with a crust of salt covering the yellowish and gray clays. The broad expanse is subject to wind erosion and the removal of vast amounts of salt during storms. While a large part of the desert is barren and without even an occasional plant to interrupt the monotony of the white surface, the area as a whole is far from being entirely barren. The pickleweed has become established in widely scattered hummocks along the broad border and in certain places in mid-desert. The samphires are scanty. Toward the surrounding hills the pickleweed increases in density, scanty growths of salt grass appear, and finally the inkweeds enter. The distribution of these plants is spotty and irregular, some places showing dense stands, but the greatest extent shows a poor, dwarfed, and wind-swept vegetation. The dual effects of climate and alkali render this area one of the most forbidding deserts on this continent, and the vegetation leading to its reclamation must meet a double problem.

Alkaline plains

The plains differ from the playas in being higher areas that do not accumulate water during the wet periods and that are otherwise well drained. For the greatest extent the soil is Jordan loam with a clay subsoil. In some areas hardpan is present as the subsoil. A few places are sandy. The water table is seldom less than 3 feet deep and in most areas 6 feet or more from the surface. Saline conditions cover a wide range and their consideration will be left for specific citation.

FLORISTICS.—The flora is diverse, often mixed, and in most regions forming certain well defined combinations that are rather constant over wide areas. Some of these combinations may be considered as associations while others less extensive and less well defined will be considered simply as plant communities. The following are recognized: greasewood-shadscale association (*Sarcobatus vermiculatus* and *Atriplex confertifolia*), shadscale association, *Kochia* flat association (*K. vestita* and *K. americana*), *Kochia-Suaeda* communities, *Sarcobatus-Grayia* communities, and rabbit-brush communities (*Chrysothamnus* spp.)

GREASEWOOD-SHADSCALE ASSOCIATION.—This is the most extensive association of the region and is second only to *Artemisia tridentata* as a basin type of vegetation. It grows in all quarters of the region, borders most parts of the Great American Desert, and is

TABLE XIII

PHYSICAL COMPOSITION OF SOILS OF GREASEWOOD-SHADSCALE ASSOCIATION IN PERCENTAGE OF PARTICLES OF DIFFERENT SIZES IN TERMS OF DRY WEIGHT AND H-ION CONCENTRATION

No.	Locality	Soil	Diameter of particles (mm.)						pH
			6	5	3	2	1	½	
166	Tooele Valley	Loam	3.5	3.0	4.3	6.1	6.5	76.6	9.4
162	Tooele Valley	Clay	0.0	0.0	0.0	0.4	1.4	98.2	9.1
107	Jordan Valley	Loam	0.0	0.2	0.2	0.2	3.5	95.9	8.6
134	Farmington	Loam	0.4	1.3	2.8	11.8	26.2	57.5	8.9

TABLE XIV

WATER AND TOTAL SALTS CALCULATED IN PERCENTAGES OF DRY WEIGHT OF SOILS FROM GREASEWOOD-SHADSCALE ASSOCIATION

No.	Locality	Soil and subsoil	Water table (ft.)	Total salts (%) at		
				1 in.	2 ft.	3 ft.
24	Jordan Valley	Jordan loam Jordan clay	3	0.83	0.82	0.83
37	" "	Jordan loam Jordan clay	3	0.75	0.82	0.82
38	" "	Jordan loam hardpan	6	0.21	0.22	0.18
39	" "	Jordan loam hardpan	6	0.26	0.18	0.18

found generally in most saline situations throughout the west. It encroaches on both pioneer and intermediate floras of the strand and playas. The general aspect presents a scrubby vegetation 3–5 feet in depth with alternating patches of the greasewood and shadscale, the greasewood being the most extensive member. This plant has a much branched stem with white shreddy bark and green wood, and numerous spiny branches with terete fleshy leaves. The roots penetrate the soil to a depth of 10–15 feet and the plant is noted as a

ground-water indicator. It is also an indicator of black alkali, sodium carbonate.

The shadscale is a round-topped bush acquiring a height of 3 feet in its robust forms. The leaves are broad and thick with a silvery coat of scurfy scales. The physical factors governing this vegetation center around the alkali content of the soil and to a less extent the depth of the water table. Soil samples were taken from many localities, most of which show the conditions to be very similar. Tables XIII and XIV show the typical ranges of conditions.

The composition of this association varies in different localities, the areas approaching the lake showing a predominance of the Chenopodiaceae while the distal margins where the alkali is reduced show an abundance of grasses and annuals. The composition is as follows:

Dominant shrubs:

Atriplex confertifolia (Torr.) Wats.
A. truncata (Torr.) Gray
A. nuttallii Wats.
Sarcobatus vermiculatus (Hook.) Torr.
Eurotia lanata (Pursh) Moq.
Kochia vestita (Wats.) A. Nels.
Suaeda moquinii (Torr.) A. Nels.
Chrysothamnus nauseosus (Pall.) Brit.
Tetradymia spinosa H. & A.

Frequent herbs:

Sclerochloa dura (L.) Beauv.
Aristida longiseta Steud.
Sitanion hystrix (Nutt.) J. G. Smith
Atriplex argentea L.
A. hastata L.
A. rosea L.
Amaranthus graecizans L.
Cleome lutea Hook.
C. serrulata Pursh
Opuntia fragilis (Nutt.) Haw.
O. polyacantha K. Sch.

Cressa erecta Rydb.
Grindelia squarrosa (Pursh) Dunal
Ambrosia psilostachya DC.
Machaeranthera leucanthemifolia Greene
Lactuca integrata (Gren. & Godr.) A. Nels.
L. scariola L.

These plants include principally the perennials and such annuals as persist until late summer. The vernal aspect is remarkable in its number and density of short-lived annuals. The most dominant members include *Bromus hordeaceus*, *B. tectorum*, *Hordeum gussonianum*, and many species of the Cruciferae. In the early spring the flats are green but by the end of June these plants form a carpet of parched, tawny brown herbage. In various sections of the greasewood-shadscale areas the density is different so that the predominance of the vernal types is variable. In dense stands of the shrubs the vernal plants are sometimes very scanty, while in areas where the shrubs are widely disposed the vernal growths are ample and rather suggest a shrubby grass flat community. The composition of the vernal flora is as follows:

Dominant species:

Bromus tectorum L.
B. hordeaceus L.
Hordeum gussonianum Parl.
Lepidium perfoliatum L.
Erodium cicutarium L'Her.

Subdominant species:

Lepidium dictyotum Gray
Hutchinsia procumbens (L.) Desv.
Capsella bursa-pastoris Medic.
Malcolmia africana (Willd.) A. Br.
Sophia pinnata (Walt.) Brit.
S. sophia L.
Camelina microcarpa Andrz.
Alyssum alyssoides (L.) Gouan.
Draba nemorosa L.
D. micrantha Nutt.

Thelypodium sagittatum (Nutt.) Endl.
Sisymbrium altissimum L.
S. asperum DC.
S. repandum L.
Lomatium platycarpum (Torr.) C. & R.
Aulospermum longipes (Wats.) C. & R.
Lappula redowskii occidentalis (Wats.) Rydb.
Castilleja linariaefolia Benth.
Adenostegia sp.
Plantago elongata Pursh
P. purshii Roem. & Schult.
Matricaria suaveolens (Pursh) Buchanan

Mosses:

Pterygoneurum cavifolium (Ehrh.) Jur.
Tortula ruralis Ehrh.
T. subulata inermis B. & S.
Pottia nevadense Card. & Ther.
Funaria hygrometrica (L.) Sibth.
F. calcarea Wahl.
Bryum caespiticium L.
B. inclinatum (Sw.) Bland.
B. pendulum (Hornsh.) Schimp.

The variety of plants is much greater on the east side of the lake than on the west side, since the east side receives about 10 inches more annual rainfall than the western part. The valleys along the southern and western sections of the lake show the association at its best. In Curlew and Hansel valleys on the northwestern borders the plants are not so robust, but present a monotonous combination of green and silvery gray for miles. The water table is remote except along the immediate lake borders. The annuals are fewer and the grasses less prominent. The dominant plants are more evenly balanced, the notable ones being as follows:

Common species:

Atriplex truncata (Torr.) Gray
A. nuttallii Wats.
A. saccaria Wats.

A. falcata (Jones) Standl.
Grayia spinosa (Hook.) Moq.
Suaeda moquinii (Torr.) A. Nels.
S. intermedia Wats.
S. diffusa Wats.
Kochia vestita (Wats.) A. Nels.
Eurotia lanata (Pursh) Moq.

Frequent species:

Eriocoma cuspidata Nutt.
Sitanion hystrix (Nutt.) J. G. Smith
Eriogonum pusillum T. & G.
Opuntia sp.
Gutierrezia microcephala Gray
Chrysothamnus nauseosus (Pall.) Brit.
Artemisia tridentata Nutt.
A. spinescens Eat.

A remarkable stand of greasewood and shadscale is found bordering the old lake shore in the Lakeside Mountain region. In most places it has the normal aspect as to depth of vegetation and density, but there is one tract which shows a relatively pure stand of large greasewoods which attain a height of 10 feet. The composition is somewhat varied by a greater abundance of *Tetradymia*, *Grayia*, and *Opuntia*.

The greasewood-shadscale association is the edaphic climax vegetation of the Great Salt Lake region. At its outer limits it is invaded mainly by *Artemisia tridentata* and by a mixed grass-shrub community of plants that is not very well defined. It is not a permanent vegetation but one of long duration. The guarantee of its persistence is alkali. Physical forces are continually but slowly reducing the salt content of the soil. The chief agencies are wind and water. The former removes vast amounts during dust storms and deposits non-saline dust from other regions; the latter tends to carry the salt in solution to the lake and deposit non-saline detritus from the hills above. The reaction of the plants to the reduction of alkali is a critical point which may be of short or long duration, depending upon conditions. Where halophytes are partially covered by flood deposits

they may persist, but new progeny are forced out by the non-saline types. The broad plains are slow in giving up the alkali, and only near the outer borders is the ingress of non-halophytes creating sharp and critical competition. The halophytes lose ground mainly through lack of progeny to maintain the hold established when saline conditions were nearer the optimum. Upsetting the equilibrium which guarantees the persistence of the halophyte reduces its relative competitive power, and thus it is forced closer and closer to the center of the alkali. It is another phase in the dynamics of vegetation which covers long periods of time. With the slow procession crowding the halophytes ever closer to the lake, and with the possible extinction of the lake, they are destined to occupy a much smaller area than they now hold. Successions in remote regions may arise and culminate, perhaps perish, before the lowest point on the Great Salt Lake basin is reclaimed by a non-halophytic vegetation climax. Whether this will ever occur can be left only to conjecture. Diastrophism may cut it short, or a change in climate may refill Great Salt Lake.

SHADSCALE ASSOCIATION.—Extensive stands of the shadscale frequently occur on the distal margins of the greasewood-shadscale associations. The general aspect presents a low shrubby vegetation, but the plants are usually rather widely disposed. It is essentially a flora of dry, mildly saline soils. Abundant ground water is necessary to support greasewood and many other halophytes, but *Kochia*, *Eurotia*, and many species of *Atriplex* have the capacity to grow in dry soils. High well drained ground and particularly long alluvial slopes are favorable for development of the shadscale association. Regions of this character are found in Tooele Valley, the valleys bordering the Great American Desert, and in Curlew Valley. *Atriplex confertifolia* is the dominant shrub. The vernal flora is much like that described in the preceding association. The composition of the summer aspect is as follows:

Shrubs:

Atriplex confertifolia (Torr.) Wats.
A. nuttallii Wats.
A. truncata (Torr.) Gray
Eurotia lanata (Pursh) Moq.
Kochia vestita (Wats.) A. Nels.

Tetradymia spinosa H. & A.
T. nuttallii T. & G.
Artemisia spinescens Eat.
Chrysothamnus pumilus Nutt.
C. nauseosus (Pall.) Brit.
Gutierrezia microcephala Gray

Herbs:

Poa sandbergii Vasey
Festuca octoflora Walt.
Bromus tectorum L.
Agropyron tenerum Vasey
Eriogonum cernuum Nutt.
E. sp.
Salsola pestifer A. Nels.
Amaranthus graecizans L.
Lepidium perfoliatum L.
Draba nemorosa L.
D. micrantha Nutt.
Arabis holboellii Hornem.
Malcolmia africana (Willd.) R. Br.
Cleome lutea Hook.
Astragalus utahensis T. & G.
Sphaeralcea grossularieafolia (H. & A.) Rydb.
Opuntia sp.
Chrysopsis foliosa Nutt.
Aster sp.
Antennaria sp.

KOCHIA FLAT ASSOCIATION.—*Kochia* is a small shrub seldom more than 1 foot high with a more or less herbaceous upper stem and a woody base. The leaves are narrow, slightly fleshy, and covered with long soft hairs. There are two species in this region, *K. vestita* and *K. americana*. The general aspect of the association is a low shrub of grayish color and relatively few associates. The ground is usually exposed more than in most associations and communities. The soil relations are shown in table XV.

Kochia is not a particularly deep rooting plant and typically feeds

on precipitation water. In nearly all places where it occurs as an association the flats are dry and well drained. Tooele, Skull, and Curlew valleys show the association at its best. Most of the associated

TABLE XV

ANALYSIS OF SOILS OF KOCHIA FLAT ASSOCIATION. SALTS IN TERMS OF DRY WEIGHT OF SOIL

No.	Locality	Soil subsoil	pH	Total salts (%) at		
				1 in.	2 ft	3 ft.
17	Skull Valley	Jordan clay	8.4	1.62	1.64	.....
17a	Skull Valley	Jordan clay	8.4	1.03	1.16	1.30
26	Jordan Valley	Jordan loam hardpan	8.2	0.26	0.27	0.26
64	Tooele Valley	Jordan loam Jordan clay	8.6	0.84	0.86	0.86

plants are the same as previously listed but occur in different degrees of abundance. The following are the commonest members:

Shrubs:

Kochia vestita (Wats.) A. Nels.
K. americana Wats.
Eurotia lanata (Pursh) Moq.
Atriplex truncata (Torr.) Wats.
A. nuttallii Wats.
Tetradymia glabrata Gray
T. spinosa H. & A.

Herbs:

Poa sandbergii Vasey
Deschampsia danthonioides Munr.
Bromus tectorum L.
Lepidium perfoliatum L.
Plantago purshii Roem. & Schult.

KOCHIA-EUROTIA COMMUNITIES.—This community is merely a rather well defined variation of the *Kochia* flat association, differing mainly in having *Eurotia* in equal dominance with *Kochia*. The community is generally denser than the preceding association but the species are about the same.

KOCHIA-SUAEDA COMMUNITIES.—This is another variation of the *Kochia* flat association, occurring in local areas of dry and rather strongly saline soil. The general aspect is darker than the preceding community, with *Suaeda depressa*, *S. diffusa*, and an occasional greasewood forming the principal members. Other species are few and widely scattered.

RABBIT-BRUSH COMMUNITIES.—As one of the most prominent plants of the lowlands, the rabbit-brush finds an important rôle in many associations and by itself often constitutes the dominant aspect in certain localities. It is essentially a ground water indicator and thrives in mildly saline soils. Its limits of tolerance vary with the type of alkali present. In the Great Salt Lake region where chlorides and carbonates are strong its range appears to be between 0.1 to 0.3%, although in local places it has been observed to grow in soils bearing as high as 0.8% salt. The Tooele Valley study (**7**) reports an average of 0.3%, while in other regions in the state it has been reported in soils of 3.15% salt (**8**). When high concentrations are found gypsum is usually the principal salt.

The most extensive rabbit-brush communities are located in Tooele and Blue Spring valleys. Frequently it is associated with greasewood or *Sporobolus*. On Stansbury Island it commonly grows with the greasewood on the flats and with the sage on the higher levels. It is one of the dominant plants of sand dunes. Scattered growths occur in nearly all parts of the region along the junction between alkaline and non-alkaline soils.

The general aspect presents a community of somewhat open growth with caespitose erect stems 3–4 feet high, the individuals rather evenly disposed. Grasses and small herbs usually occupy the intervening spaces. The composition is as follows:

Principal species:

Chrysothamnus pinifolius Greene
C. viscidiflorus tortifolius (Gray) Greene
C. nauseosus (Pall.) Brit.
C. puberulus (Eat.) Greene
C. graveolens (Nutt.) Greene
C. pulcherrimus Greene

Sporobolus airoides (Torr.) Gray
Distichlis spicata (L.) Greene

Frequent species:

Bromus tectorum L.
Allium acuminatum Hook.
Zygadenus paniculatus Wats.
Comandra pallida DC.
Kochia vestita (Wats.) A. Nels.
Atriplex hastata L.
A. confertifolia (Torr.) Wats.
Eurotia lanata (Pursh) Moq.
Sarcobatus vermiculatus (Hook.) Torr.
Suaeda moquinii (Torr.) A. Nels.
Lepidium perfoliatum L.
Camelina microcarpa Andrz.
Sophia sophia L.
Malcolmia africana (Willd.) R. Br.
Erodium cicutarium L'Her.
Opuntia fragilis (Nutt.) Haw.
Grindelia squarrosa (Pursh) Dunal
Aster leucanthemifolius Greene
Artemisia tridentata Nutt.
A. gnaphalodes Nutt.
Cirsium scariosum Nutt.
Lactuca integrata (Gren. & Godr.) A. Nels.

Dunes

The dunes of Great Salt Lake are formed of two kinds of sand, calcareous oolitic sand and fine-grained siliceous sand. Considerable stress was laid on the formation of calcareous deposits through the precipitation of calcium carbonate from the lake waters in the earlier part of this paper. All of the dunes bordering the lake are of the calcareous type while those removed from the lake are of the siliceous type.

SALTAIR SECTION.—Extending from Saltair to the Jordan Delta is a series of low dunes of calcareous character. The grains are coarse and often mixed with a stony element derived from hardpan. The

finer material shows more than 98% particles less than 0.5 mm. in diameter by dry weight, while the coarser material averages a little over 50% particles of this size. The alkali content is shown in table XVI.

The general aspect presents the light colored oolitic and hardpan material dotted with shrubs and tufts of grass while a variety of small herbs are scattered between. The greasewood and rabbit-brush are the dominant shrubs and *Eriocoma* and *Sporobolus* the dominant

TABLE XVI

WATER AND CHEMICAL ANALYSIS OF OOLITIC DUNE DEPOSIT OF SALTAIR SECTION. SALTS CALCULATED IN TERMS OF DRY WEIGHT OF SAMPLES

DEPTH	WATER CONTENT	NaCl	Na_2CO_3	$NaHCO_3$	Na_2SO_4	TOTAL SALTS
4 in.	4.59	0.16	0.057	Trace	0.497	0.62
2 ft.	12.81	0.255	0.100	0.01	0.284	0.64

herbs. In local depressional areas the salt grass, samphires, and inkweeds become prominent. The older dunes show a mixed plant community with both halophytic and non-halophytic plants growing together with no apparent diminution in vigor or robustness. The composition is as follows:

Shrubs:

Atriplex confertifolia (Torr.) Wats.
A. canescens (Pursh) James
A. truncata (Torr.) Gray
Sarcobatus vermiculatus (Hook.) Torr.
Gutierrezia microcephala Gray
Chrysothamnus pulcherrimus Greene

Frequent herbs:

Eriocoma cuspidata Nutt.
Sporobolus airoides Torr.
Distichlis spicata (L.) Greene
Bromus tectorum L.
Poa sp.
P. sandbergii Vasey

Sitanion hystrix (Nutt.) J. G. Smith
Atriplex hastata L.
Salsola pestifer A. Nels.
Abronia salsa Rydb.
Sphaerostigma utahensis Small
Chaenactis stevioides H. & A.

STANSBURY ISLAND DUNES.—On the west side of the island extending from the middle to the northern extremity is a series of dunes. It varies in width up to nearly 300 yards and varies in depth up to 15 or 18 feet. The sand is of the oolitic calcareous type, white on the surface, but at 2 or 3 feet in depth it is of finer texture and brownish in color. There is also a siliceous element at this depth. At the northern end the light material has been blown high up on the rocky hillside. Presumably the deposits rest on a level saline plain.

The floral aspect is dominated by two plant types. The southern part shows a scattered shrub community dominated by greasewood and rabbit-brush while toward the north *Juniperus utahensis* offers an interesting and unique situation. Many typical dune species are to be noted in *Eriocoma*, *Eriogonum*, *Abronia*, and the Onagraceae. The moss *Tortula ruralis* may be properly classed as a dominant member, great tufts occurring frequently under shrubs and on the north-facing slopes.

The shrubby areas may be traced by the prominent white color of *Chrysothamnus puberulus*, which is robust in habit and lends a distinct character to the vegetation as a whole. The composition of the shrubby community is as follows:

Dominant shrubs:

Sarcobatus vermiculatus (Hook.) Torr.
Atriplex canescens (Pursh) James
Chrysothamnus puberulus (Eat.) Greene

Frequent shrubs:

Grayia spinosa (Hook.) Moq.
Chrysothamnus lanceolatus Nutt.
C. stenophyllus (Gray) Greene
C. viscidiflorus (Hook.) Nutt.
C. viscidiflorus tortifolius (Gray) Greene

Frequent herbs:

Eriocoma cuspidata Nutt.
Sporobolus cryptandrus (Torr.) Gray
Bromus tectorum L.
Agropyrum tenerum Vasey
Elymus condensatus Presl.
Comandra pallida DC.
Eriogonum cernuum Nutt.
E. ovalifolium Nutt.
Salsola pestifer A. Nels.
Abronia fragrans Nutt.
A. micrantha Torr.
Erysimum sp.
Astragalus utahensis T. & G.
Mentzelia acuminata (Rydb.) Tidest.
M. laevicaulis (Dougl.) T. & G.
Pachylophus sp.
Sphaerostigma utahensis Small
Ptiloria exigua (Nutt.) Greene
Chylisma parryi (Wats.) Small
Leptodactylon pungens (Torr.) Wats.

The depressions are more alkaline, as indicated by the presence of *Distichlis* and *Sporobolus*. *Bryum* sp. is also found here.

The northern half of the dunes shows the entrance of the juniper, which is slowly invading the shrubby communities, the first entrants being small and shrubby. The species just listed persist, although fewer in numbers, as the junipers become more and more dominant. As the dunes become larger the trees increase in size and numbers in proportion. In addition to the plants cited, the juniper community has the following:

Juniperus utahensis (Engelm.) Sarg.
Hordeum pusillum Nutt.
H. maritimum With.
Chenopodium album L.
Atriplex rosea L.
Erodium cicutarium L'Her.
Rhus trilobata Nutt.

The presence of the juniper is a point of special interest in that it marks the closest approach of trees to the lake. Its tolerance of mild concentrations of alkali is well known in other parts of the state, where it reaches its maximum development.

LAKESIDE MOUNTAIN DUNES.—One of the most interesting dune areas is that paralleling the base of the Lakeside Mountains, about 2 miles from the old lake shore. They are mainly siliceous and of a very fine tan-colored sand. While their origin is obscure, they may have been calcareous dunes at one time and have since had the calcium washed away, leaving the siliceous nuclei of the original oolite.

Sarcobatus and *Atriplex canescens* are the commonest shrubs. The open places show many characteristic species, among which are *Eriocoma*, *Eriogonum cernuum*, *Rumex venosus*, *Abronia salsa*, *A. cycloptera*, a species of *Psoralea*, and *Chamaesyce flagelliformis*. The following list shows the composition:

Shrubs:

Atriplex canescens (Pursh) James
A. confertifolia (Torr.) Wats.
Grayia spinosa (Hook.) Moq.
Chrysothamnus viscidiflorus tortifolius (Gray) Greene
Artemisia tridentata Nutt.
Tetradymia spinosa H. & A.

Frequent herbs:

Eriocoma cuspidata Nutt.
Sitanion hystrix (Nutt.) J. G. Smith
Eriogonum cernuum Nutt.
Rumex venosus Pursh
Chenopodium album L.
C. fremontii Wats.
C. sp.
Atriplex rosea L.
Amaranthus graecizans L.
Abronia salsa Rydb.
A. cycloptera Gray
Erysimum sp.
Cleome lutea Hook.

Psoralea lanceolata Pursh (?)
Chamaesyce flagelliformis (Engelm.) Rydb.
Opuntia fragilis (Nutt.) Haw.
Oenothera sp.
Chylisma parryi (Wats.) Small
Leptodactylon pungens (Torr.) Nutt.
Cryptanthe sp.
Solanum triflorum Nutt.
Marrubium vulgare L.
Machaeranthera sp.
Ptiloria exigua (Nutt.) Greene
Helianthus annuus L.

Tortula ruralis is the only moss.

Salt marshes and sloughs

Salt marshes and sloughs may arise in a variety of ways. They occur in localities where the water table is very close to the surface, where fresh water or saline springs and wells have their outlets. Tooele, Jordan, and Malad valleys are the principal localities, while numerous smaller areas are to be found in other places.

Analyses of the soils from the margins and beds of marshes and sloughs show conditions to be much like those already cited. Toward the outer limits of the alkali belt all gradations of saline quality of the soil may be observed, from those strongly impregnated with alkali to those that are comparatively sweet. The H-ion concentration of both soil and water shows much the same reactions as noted before. Table XVII gives a list of localities and the pH concentrations. Analyses of the waters from the principal mineral springs are given in the section dealing with hot mineral springs.

BLACK ROCK-TOOELE VALLEY MARSHES.—Topography plays a rôle in some places. At Black Rock, springs are found along the base of a steep headland so that extremes in alkalinity are found within a very short range. Southward and entering Tooele Valley the marshes are established in the depressions. The floral aspects are much the same as in most marshes in this region, with rushes and cattails lending the usual dominating characteristics. The features of contrast are noted mainly in subsidiary types. In this instance the

algae are of particular interest, showing types that are adjusted to mildly saline water. Among the specimens collected are two species of *Enteromorpha* which are abundant in some places and *Spirogyra*

TABLE XVII

H-ION CONCENTRATION OF SOILS AND WATERS FROM VARIOUS SALT MARSHES, SLOUGHS, AND SPRINGS OF GREAT SALT LAKE REGION

No.	Type of vegetation	Locality	Soil or water	pH
157	Batrachospermum	Jordan Valley	Spring water	7.4
154	Radicula, Glaux, Glycyrrhiza	" "	Black loam	7.8
155	Scirpus olneyi	" "	" "	8.6
156	Sporobolus	" "	" "	7.6
105a	Cladophora, etc.	" "	Well water	7.6
105	Distichlis	" "	Slough clay	8.8
100	River water	Jordan River	Water	8.0
135	Distichlis	Farmington	Slough clay	8.5
188	Barren	Jordan Valley	Slough bed	8.4
189	Allenrolfea	" "	Slough margin	8.6
190	Suaeda occidentalis, Bryum, etc.	" "	" "	8.4
191	Allenrolfea	" "	" "	9.2
193	Distichlis	" "	" "	8.6
194	Chara, Typha, Scirpus	" "	Salt marsh	8.6
195	Distichlis, Sida, etc.	" "	Marl loam	8.4
196	Atriplex hastata	" "	" "	8.2
197	Scirpus, Aster angustus, etc.	" "	" "	8.2
199a	Myxophyceae	" "	Well water	8.3
202	Scirpus paludosus	" "	Slough bed	8.5
203	Distichlis, Suaeda	" "	" "	8.3
204	Myxophyceae	" "	Hot spring	8.4

and *Cladophora* which are abundant in other places. The algal flora is:

Myxophyceae:

Aphanothece nidulans Rich.
Tolypothrix tenuis Kz.

Chlorophyceae:

Chlamydomonas spp.
Cladophora spp.
Enteromorpha intestinalis L.
E. plumosa Kz.

Potamogeton pectinatus was the only submerged vascular plant found. The emergent members form dense and extensive societies. The rushes are most prevalent in the more strongly saline portions

of the marsh while cattails are restricted to the margins where the salt is not so concentrated. The following plants were listed:

Typha latifolia L.
T. angustifolia L.
Scirpus americanus Pers.
S. lacustris L.
S. olneyi Gray
S. paludosus A. Nels.
Eleocharis palustris (L.) R. & S.

The muddy banks generally show a mixture of true halophytes and plants of sweet soils. The grasses are usually dominant. This society includes:

Eleocharis acicularis (L.) R. & S.
Polypogon monspeliensis (L.) Desf.
Distichlis spicata (L.) Greene
Puccinellia nuttalliana (Schultes) Hitchc.
Juncus balticus Willd.
Carex nebraskensis Dewey
Rumex persicarioides L.
R. crispus L.
Atriplex hastata L.
Halerpestes cymbalaria (Pursh) Greene
Radicula nasturtium-aquaticum (L). Brit. & Rendle
Cicuta occidentalis Greene
Berula erecta (Huds.) Coville

Conjunctive with the marshes are meadow-like societies harboring many grasses and a wide variety of other plants. The components include:

Triglochin maritima L.
T. palustre L.
Sporobolus asperifolius (Nees & Mey.) Thurb.
S. airoides Torr.
S. confusus (Fourn.) Vasey
Polypogon monspeliensis (L.) Desf.
Spartina gracilis Trin.
Beckmannia erucaeformis (L.) Host.

Phragmites communis Trin.
Puccinellia nuttalliana (Schultes) Hitchc.
Hordeum jubatum L.
Bromus tectorum L.
Distichlis spicata (L.) Greene
Juncus balticus Willd.
Rumex persicarioides L.
R. crispus L.
R. britannica L.
Atriplex hastata L.
Bassia hyssopifolia (Pall.) Kuntze
Abronia salsa Rydb.
Myosurus apetalus Gay
Ranunculus eremogenes Greene
Halerpestes cymbalaria (Pursh) Greene
Spergularia rubra (L.) J. & C.
S. salina Presl.
Glaux maritima L.
Dodecatheon salinum A. Nels.
Gaura parviflora Dougl.
Onagra hookeri (Torr. & Gray) Small
Asclepias speciosa Torr.
Castilleja stricta Rydb.
Adenostegia ramosa (Nutt.) Greene
Iva axillaris Pursh
Helianthus annuus L.

The abrupt slopes of the headlands make a narrow conjunctive belt with the marshes and springy areas which is much reduced in alkali content so as to present a different community of plants:

Hordeum jubatum L.
Salix exigua Nutt.
Urtica breweri Wats.
Atriplex rosea L.
Sophia pinnata (Wats.) Brit.
Sisymbrium altissimum L.
Cleome serrulata Pursh

Rosa melina Greene
Melilotus alba Desv.
Trifolium repens L.
Glycyrrhiza lepidota Pursh
Rhus trilobata Nutt.
Onagra hookeri (T. & G.) Small
Berula erecta (Huds.) Coville
Asclepias speciosa Torr.
Cuscuta sp. on Helianthus et al.
Cressa erecta Rydb.
Marrubium vulgare L.
Castilleja linariaefolia Benth.
C. exilis A. Nels.
Rubia tinctoria L.
Grindelia squarrosa (Pursh) Dunal
Iva axillaris Pursh
Ambrosia psilostachya DC.
Xanthium pennsylvanicum Wallr.
Helianthus annuus L.
Helenium autumnale L.
Crepis runcinata T. & G.
Lactuca integrata (Gren. & Godr.) A. Nels.
L. scariola L.

Malad Valley and Blue Spring Hills section.—This region includes extensive marsh lands, many of which have been extended artificially for the purpose of maintaining them as bird sanctuaries. As in the case of the river deltas, several plants beneficial to birds have been introduced. *Ruppia*, *Potamogeton*, *Sparganium*, *Puccinellia*, and several rushes are the principal ones. In general these marshes are similar in plant types although they differ in minor respects. The following species were peculiar to this section:

Sparganium eurycarpum Engelm.
Lemna minor L.
Spirodela polyrhiza (L.) Schleich.
Potamogeton natans L.
Ruppia maritima L.

Echinochloa crus-galli (L.) Beauv.
Scirpus validus Vahl.
Carex stipata Willd.
Polygonum emersum (Michx.) Brit.
Epilobium adenocaulon Hausskn.
Helianthus nuttallii T. & G.

Sloughs

Sloughs occur chiefly in Jordan Valley. They differ from the marshes in being poorly drained, are generally more saline, and the grasses replace the rushes and cattails as the dominant types. There are numerous plants distributed in many families. The bottoms are muddy with flocculent masses of black muck consisting of finely divided vegetal matter mixed with clay. The algal flora of these situations is of particular interest. In general those areas strongly alkaline have a preponderance of Myxophyceae while localities less alkaline show a decided increase in Chlorophyceae. Wherever sloughs are maintained by wells or springs of mineral water Myxophyceae are also the dominating algae. The following is a composite list:

Myxophyceae:

Oscillatoria amphibia Ag.
O. animalis Ag.
O. amoena (Gom.) Kz.
O. chalybea Mert.
O. janthophora
O. nigro-viridis Thw.
O. subtilissima Kuetz.
O. spp.
Phormidium angustissimum W. & G. S. West
P. foveolarum (Gom.) Mont.
P. fragilis Menegh.
P. ramosum P. Boye
Aphanothece calthrata West
A. nidulans Rich.
Anabaena spp.
Lyngbya martensiana Menegh.

L. aeruginea-caerulea (Kuetz.) Gom.
Tolypothrix tenuis Kz.
Nostoc pruniforme (L.) Ag.
N. spp.

Chlorophyceae:

Ulothrix zonata (?)
U. spp.
Spirogyra spp. (five species indet.)
Zygnema spp.
Oedogonium spp.
Rhizoclonium hieroglyphicum Kz.
Nephrocystium agardhianium Nag.
Gloeocystopsis limneticus Am.
Cladophora fraeta forma
C. spp.
Enteromorpha intestinalis L.
E. plumosa Kz.

Rhodophyceae:

Batrachospermum spp.

Charaphyceae:

Chara foetida L.
C. fragilis ?

Several other species were included in the collections to which no definite names could be assigned. This was particularly true of the unicellular forms.

Among the vascular plants the grasses are the dominant types, the salt grass being almost exclusive in this respect in most localities. Most of the species listed for the marshes occur on the margins of adjacent areas. Besides the plants listed previously the following were noted for the sloughs alone:

Poa nevadensis Vasey
Elymus glaucus Buckley
E. triticoides Buckley
Juncus nevadensis Wats.
Polygonum ramosissimum Michx.

P. convolvulus L.
P. aviculare L.
Chenopodium album L.
C. glaucum L.
C. leptophyllum (Moq.) Nutt.
Atriplex falcata (Jones) Standl.
A. nitens
Suaeda depressa (Pursh) Wats.
S. intermedia Wats.
S. moquinii (Torr.) A. Nels.
Amaranthus blitoides Wats.
Sesuvium sessile Pers.
Lepidium perfoliatum L.
Sida hederacea (Dougl.) Torr.
Apocynum cannabinum L.
Asclepias incarnata L.
Cressa erecta Rydb.
Marrubium vulgare L.
Aster frondosus (Nutt.) T. & G.
A. angustus T. & G.

Hot mineral springs

Hot springs are found along the base of the Wasatch Mountains and at the south end of the Blue Spring Hills. The origin of these springs is believed to have been brought about through faulting in which a great amount of heat was generated by the friction. The great depth serves as insulation while the crushed rocks along the fault plane serve to collect percolating waters.

The temperature of the water varies from 34° to 61° C. While sulphurous in quality the dominant constituent is sodium chloride in every case. The H-ion concentration varies from 8.2 to 8.8. Analyses of the most important springs are given in table XVIII. The discharge from some of these springs is considerable, the largest two being Beck's Hot Spring and a spring near the town of Honeyville. The water wells up in great volume with a characteristic sulphurous odor.

The flora of the springs proper is exclusively of Myxophyceae

while in the outlets a limited number of Chlorophyceae and vascular plants occur. There is a rather marked uniformity in the species inhabiting the various springs, although the larger springs show the richest and most varied flora. *Oscillatoria amphibia* and *O. animalis*

TABLE XVIII

ANALYSES OF WATERS FROM HOT MINERAL SPRINGS OF GREAT SALT LAKE REGION, IN TERMS OF P.P.M., EXCEPT D WHICH IS PERCENTAGE (2)

	A	B	C	D	E	F	G
Ca	694.3	141.5	535.2	4.90	901.0	1174.0	878.0
Mg	109.5	27.7	138.4	0.4	218.0	28.0	379.0
Na	3754.9	405.0	3039.0	30.38	16595.0	8563.0	10426.0
K	196.9	55.0	178.0	3.76			
Al_2O_3	9.0	.....	.....	0.02	.....	.....	.....
Fe_2O_3	.....	5.1	0.7	.....	.....	.....	.....
SiO_2	31.5	50.5	21.3	0.20	.....	.....	.....
SO_4	840.5	53.8	787.5	0.94	497.0	203.0	20.0
HCO_3 / CO_2	204.8	272.7	442.9	0.61	454.0	186.0	393.0
Cl	6743.8	635.6	4968.0	58.79	27081.0	15079.0	18460.0
Fe	.....	.....	.....	.....	1.0	1.0	2.0
Total	12584.9	1658.0	10284.0	23309.0	45541.0	25300.0	30440.0

A. Beck's Hot Spring, Temp. 133°F. BRIGGS, B. R., U.S.G.S. Bull. 42. 148. 1878.
B. Sandy Hot Springs, 8 miles south of Salt Lake City. KINGSBURY, J. T., 1882.
C. Warm Springs, Salt Lake City. KINGSBURY, J. T., 1881.
D. Utah Hot Springs, 8 miles north of Ogden. Temp. 55° C. CLARKE, F. W., U.S.G.S. Bull. 9. 30. 1884.
E. Hot Spring at Honeyville, Boxelder Co. BAILEY, J. R.
F. Sanitarium Hot Springs, Boxelder Co. BAILEY, J. R.
G. Hot Spring at south end of Little Mountain (north of Bear River Bay). BAILEY, J. R.

were found in every spring investigated. The following is a composite list of all the springs:

Oscillatoria amphibia Ag.
O. amoena (Gom.) Kuetz.
O. animalis Ag.
O. brevis var. neapolitana (Kuetz.) Gom.
O. chalybea Mert.
O. janthophora
O. laetevirens Crouan.
O. lemmermannii Wolosz.

O. nigro-viridis Thw.
O. subtilissima Kuetz.
O. tenuis Ag.
Phormidium autumnale (Ag.) Gom.
P. angustissimum W. & G. S. West
P. foveolarum (Mont.) Gom.
P. ramosum P. Boye
Spirulina calderia Tild.
Lyngbya martensiana Menegh.
L. aerugineo-caerulea (Kuetz.) Gom.
Synechococcus spp.

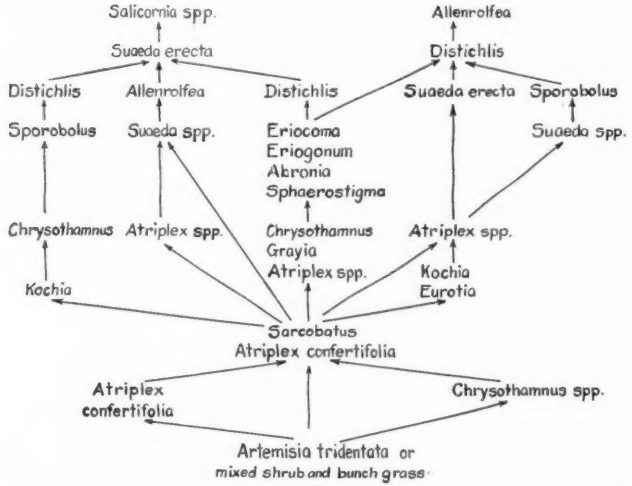

FIG. 1.—Diagram representing principal succession encroaching on strands and playas of Great Salt Lake.

Summary of successional aspects and floristics

There are two pioneer types of the halosere in this region, *Salicornia* and *Allenrolfea*. The former is most commonly followed by *Suaeda erecta* and the latter by *Distichlis*. It is of interest to note that *Salicornia* and *Allenrolfea* do not ordinarily grow together as invaders of the barren flats, but are not uncommonly associated some distance from the line of invasion. The plants making up the belts or zones succeeding are so various that it is difficult to select

any one or two types as representative of the region. *Distichlis*, *Sporobolus*, species of *Suaeda* and of *Atriplex* cover such a wide and diverse area that tracing a uniform line is almost impossible. They occur in nearly every combination as the intermediate successional stage. The diagram shown in figure 1 shows the actual successions of some of the larger and representative localities from various points around the lake.

The floristic features are tabulated in tables XIX and XX. In the first are listed the number of species in each family showing four relative degrees of halophytism. Column I includes all those that are absolute halophytes found only in alkaline soil; column II includes plants essentially halophytes but with a wide range of toleration; column III is a group of plants essentially non-halophytic but frequently inhabiting saline areas; column IV includes such plants as are seldom found in halophytic regions. According to this estimate, 54.3% of the flora is essentially halophytic and 45.7% essentially non-halophytic but with a certain degree of alkali tolerance.

Table XX indicates the geographic relations as to extent of distribution. The endemic species are those occurring only within a 100-mile radius of Great Salt Lake; the western species are those of the Rocky Mountain region and westward. A little over half of the flora is typically western.

Summary

1. The rocks of the Great Salt Lake region embrace a wide range of igneous, sedimentary, and metamorphic members. Historically they extend from the Archean to the Eocene, with nearly every period represented.

2. Great Salt Lake had its origin in a large Pleistocene lake named Lake Bonneville. It covered an area of 19,750 square miles and at its highest level stood about 1000 feet above the present level of Great Salt Lake. It was partially drained by erosion of the outlet and then by evaporation and seepage.

3. The climate shows an annual precipitation of about 6–7 inches in the western portion of the region and about 16–17 inches in the eastern portion. Evaporation amounts to about 68.67 inches a year, with an average wind movement of 69,139 miles yearly. The growing season free from frost averages approximately 160 days and the annual average temperature is about 50° F.

TABLE XIX

	I	II	III	IV	TOTAL
Pinaceae			1		1
Gnetaceae			2		2
Typhaceae			2		2
Sparganiaceae			1		1
Lemnaceae				1	1
Naiadaceae		2	1	1	4
Juncaginaceae			2		2
Alismaceae			2		2
Gramineae	7	14	12	5	38
Cyperaceae	2	7	4		13
Juncaceae		1	2		3
Liliaceae				3	3
Melanthaceae			1		1
Salicaceae				3	3
Urticaceae			2		2
Polygonaceae		3	7	3	13
Chenopodiaceae	22	8			30
Amaranthaceae		1	1	1	3
Nyctaginaceae		3	2		5
Aizoaceae	1				1
Caryophyllaceae	1	1			2
Ranunculaceae	1	1	3	1	6
Cruciferae		14	6	3	23
Capparidaceae		2		1	3
Rosaceae				1	1
Pomaceae				1	1
Leguminosae		3	6	1	10
Geraniaceae			1		1
Euphorbiaceae		1	2		3
Anacardiaceae				1	1
Malvaceae	1	3			4
Loasaceae			1	2	3
Cactaceae		2	2		4
Onagraceae	1	4	3	2	10
Haloragidaceae				1	1
Umbelliferae		1	5	2	8
Primulaceae	2				2
Apocynaceae			1	1	2
Asclepiadaceae		1	3	1	4
Cuscutaceae					1
Convolvulaceae	2		2		4
Polemoniaceae		2	1	3	6
Boraginaceae	2	3		1	6
Verbenaceae			1	1	2
Labiatae		1		1	2
Solanaceae		2			2
Scrophulariaceae	1	2	2	3	8
Orobanchaceae			1		1
Plantaginaceae		2		1	3
Rubiaceae			1		1
Compositae	1	42	16	12	71
Total	44	130	94	59	326
Percentage	13.5%	40.8%	27.9%	17.8%	

TABLE XX

	Endemic	Western	North American	Cosmopolitan	Disjunct
Pinaceae		1			
Gnetaceae		2			
Typhaceae				2	
Sparganiaceae				2	
Lemnaceae				1	
Naiadaceae				4	
Juncaginaceae				2	
Alismaceae			1	2	
Gramineae		13	12	13	1
Cyperaceae		1	4	8	
Juncaceae			1	2	
Liliaceae		3			
Melanthaceae		1			
Salicaceae			3		
Urticaceae		1	1		
Polygonaceae		3	3	7	
Chenopodiaceae	2	18	4	5	1
Amaranthaceae		1		2	
Nyctaginaceae		4	1		
Aizoaceae		1			
Caryophyllaceae		1	1		
Ranunculaceae		3	2	1	
Cruciferae		8	4	10	1
Capparidaceae			2	1	
Rosaceae		1			
Pomaceae	1				
Leguminosae	1	3	1	5	
Geraniaceae				1	
Euphorbiaceae		1		2	
Anacardiaceae		1			
Malvaceae		3	1		
Loasaceae		3			
Cactaceae		3	1		
Onagraceae	1	8		1	
Haloragidaceae				1	
Umbelliferae		5	2	1	
Primulaceae		1		1	
Apocynaceae				2	
Asclepiadaceae		3	2		
Convolvulaceae		2			
Polemoniaceae		6			
Boraginaceae		6			
Verbenaceae			1	1	
Labiatae			2		
Solanaceae		1		1	
Scrophulariaceae		5		3	
Orobanchaceae		1			
Plantaginaceae			2	1	
Rubiaceae				1	
Compositae	4	45	9	13	
Total	9	160	59	97	3
Percentage	2.4%	48.7%	18.1%	29.2%	0.6%

4. At present Great Salt Lake is about 75 miles long and 38 miles wide, with an average depth of 15 feet, the deepest point being about 40 feet. The brine consists principally of sodium chloride with smaller amounts of potassium, magnesium, and calcium salts. The percentage varies with the fluctuation of lake level, showing approximately 1% for every foot increase or decrease. At its highest level it showed 13.8% and at its lowest level 27.72%.

5. Floristically the region is characterized by the absence of trees, by broad barren salt flats bordered with succulent salt plants, and by a low shrubby vegetation on the saline plains.

6. The lake water proper harbors six species of algae, four Myxophyceae and two Chlorophyceae. *Aphanothece utahensis* and *Microcystis packardii* are the commonest species and are directly concerned with the formation of a tufa-like deposit which later forms a hardpan. *Chlamydomonas* sp. is abundant also.

7. The strand flora consists mainly of two invading genera, *Salicornia* and *Allenrolfea*. The former tolerates salt up to 6%, the commonest amounts being about 3% at the optimum. The latter averages between 1 and 1.5% at the optimum.

8. The strand succession is represented generally by the following zonation:

Zone 1. Salicornia rubra
S. utahensis
Allenrolfea occidentalis
Zone 2. Suaeda erecta
Zone 3. Distichlis spicata
Zone 4. Suaeda spp.
Zone 5. Sporobolus spp.
Atriplex spp.
Sarcobatus vermiculatus
Chrysothamnus spp.

9. Strand swamp types include *Scirpus americanus*, *S. paludosus*, *Potamogeton pectinatus*, *Ruppia maritima*, *Polypogon monspeliensis*, *Puccinellia nuttalliana*, and a variety of other plants.

10. The river deltas are modified by human agency and cultivation. Species of *Scirpus* predominate in most places while *Sparganium*, *Potamogeton*, *Typha*, and numerous salt marsh plants constitute a rich flora.

11. The strands of Great Salt Lake are bordered for their greatest extent by playas and alkaline plains with a few rocky headlands.

12. The soil is dominantly Jordan clay and Jordan loam with a clay or hardpan subsoil. The water table ranges from less than 3 feet to remote depths, but usually not far below 10 feet in most places.

13. The alkali relations are intimately connected with the water table. In general the percentage of alkali is roughly proportional to the depth of the permanent water, as follows:

Depth of the water table	Percentage alkali
3 feet or less	3% or more
6 feet	1–3%
10 feet	0.25–1%

The H-ion concentration of the soils ranges from pH 8.0 to 9.4, the general average being pH 8.4 to 8.6.

14. The range of alkali toleration by the principal pioneer plants is:

	Maximum	Optimum	Minimum
Salicornia	6%	2–3%	0.5–1%
Suaeda erecta	4%	1–2%	0.25%
Allenrolfea	3%	1–1.5%	0.25%
Distichlis	2%	0.7–1%	0.25%

15. The vegetation of the playa-plains region is dominated by low shrubs of silvery gray and dark green color and numerous small annuals. There are a few algae, lichens, and mosses but no liverworts nor pteridophytes. Trees are absent.

16. Playas are invaded by the following succession of plants: *Salicornia rubra*, *S. utahensis*, *Suaeda erecta*, *Allenrolfea occidentalis*, *Distichlis spicata*, numerous small herbs in the Graminaceae and Cruciferae, and finally *Sarcobatus vermiculatus* and species of *Atriplex*.

17. Playas may be reclaimed almost exclusively by a single species. Homogeneous situations may show *Salicornia* flats, *Allenrolfea* flats, *Distichlis* meadows, or *Sporobolus* fields. In contrast the playas may be reclaimed by a mixed vegetation.

18. The alkaline plains show an average range of 0.6 to 1% alkali in the soil.

19. The following associations are well defined: greasewood-

shadscale, *Sarcobatus vermiculatus-Atriplex confertifolia*, forming the dominant vegetation; shadscale association, *Atriplex confertifolia; Kochia* flat association. Less well defined are the following plant communities: *Kochia-Eurotia*, *Kochia-Suaeda*, *Sarcobatus-Grayia*, and *Chrysothamnus* spp.

20. Dunes show a characteristic vegetation of *Sarcobatus*, *Atriplex* spp., *Chrysothamnus* spp., and a number of herbaceous species typical of sandy situations.

21. Salt marshes and sloughs show numerous algae and aquatic plants typical of mildly saline water. *Scirpus* spp., *Typha*, *Distichlis*, *Juncus*, *Eleocharis*, and a variety of herbs are the principal plants.

22. Hot mineral springs carry salt up to 5% and vary in temperature up to 61° C. Myxophyceae are the only plants. *Oscillatoria* spp. are dominant.

Critical determinations of the vascular plants were made by Dr. A. O. GARRETT, Dr. P. A. RYDBERG, and Dr. F. S. BLAKE. Dr. A. J. GROUT checked some of the mosses and Dr. N. L. GARDNER named most of the algae. Thanks are due to Dr. H. C. COWLES and Dr. G. D. FULLER for their criticisms.

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SEROLOGICAL STUDIES OF PLANT VIRUSES

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Introduction

The discovery of viruses as supposedly different infectious agents has led to a problem of classification, the difficulty of which has become increasingly apparent.

Since the viruses could not be visually or culturally identified, they came to be characterized largely by what they did, that is, by the reactions they produced in the plant; and it became the custom to name the virus on the basis of the symptoms it produced on a single host (for example, tobacco mosaic, tomato mosaic, or cucumber mosaic). Confusion arose when later experiments showed: (1) that the symptoms produced by a given virus on a given plant vary with the source and mode of infection, the variety of the plant, its age, and the environment in which it has grown; (2) that the symptoms produced by a given virus may vary in different plants; and (3) that different viruses may produce similar symptoms on the same plant. Obviously a more reliable method of differentiation and classification of plant viruses is needed.

JOHNSON and HOGGAN (**6**) recommend that the present system be abandoned and an attempt be made to devise some system more comparable with the one used in classifying bacteria and fungi. Our knowledge, however, is as yet insufficient for classifying viruses, since present methods of study have yielded little positive information concerning their nature or characteristic properties which are of value in grouping them (**10**).

It has been shown that living things, plant and animal, by virtue of their chemical constituents have antigenic specificities which characterize the species, and that these antigenic specificities can be studied most advantageously by means of immunological or serological reactions. This approach has proved valuable in the study of the relationships, pathogenic properties, and chemical constituents of microorganisms (**13**), and might yield valuable information when applied to the classification of plant viruses.

The major difficulty in the use of these methods is that of securing a suitable preparation of the virus antigen. Since viruses cannot be grown in artificial mediums, it is difficult to secure antigens satisfactory in regard to purity and concentration. Such crude antigens as the extract of plant tissue contain antigenic substances other than the virus, which must be considered in interpreting the results. The few serological studies on plant viruses already made, however, although confined to the use of crude extracts and limited largely to the virus of tobacco mosaic, suggest that this method has possibilities.

Using the precipitin test, DVORAK (**3**) has shown that mosaic of potato affects the antigenic specificity of the globulin fraction of the cell juice and the cytoplasm. PURDY (**8, 9**) has shown that the juices from healthy plants and from plants affected with mosaic have antigenic substances in common. The juice of pathic tobacco plants contained an additional fraction which could not be removed from the homologous antiserum by absorption with healthy plant antigen. After such absorption, the anti-mosaic serum reacted with the juice (antigen) of tomato, petunia, pepper, and several species of tobacco, all of which had been infected with the virus of tobacco mosaic but not with the juice from healthy plants of these species. PURDY concludes from these results that the antigenic fraction which is present in the diseased plants and absent in healthy ones represents the virus, and not an altered host protein as was concluded by DVORAK. The work of MATSUMATO and SOMAWAZA (**7**) on tobacco mosaic substantiates PURDY'S conclusions. These workers found that when the juice from tobacco and tomato plants affected with mosaic was digested with trypsin and used as a test antigen, reactions were not obtained with healthy plant antiserum but were obtained with mosaic plant antiserum. The tryptic digest was infectious, indicating that, although the healthy plant proteins were apparently broken down so far that they no longer acted as antigens, the virus had withstood the trypsin sufficiently to remain antigenic.

The characteristic antigenic property of a virus-diseased plant as reported by these workers might be due to (1) alteration by the virus of the normal healthy antigenic constituents of the plant, (2) linkage of the virus to the normal healthy constituents of the plant,

or (3) the virus itself. This paper deals with an attempt to determine which of the foregoing factors is responsible for the specificity of the serological reactions, and whether these reactions can be used in differentiating and classifying plant viruses.

Part I

Problem

An attempt was made to determine whether the characteristic specificity of the serological reactions with plant virus is due to alteration of the normal healthy antigenic constituents of diseased plants or to the virus itself.

It was thought that purification of the virus by methods which involved different principles and testing of these preparations by the precipitin technique might produce evidence on the specificity of the reaction for the virus. In order to prepare serologically pure antigens it is necessary to remove contaminating antigenic substances. Since the preponderance of evidence indicates that only proteins or protein complexes can function as true antigens, it follows that the removal of plant proteins is of paramount importance in preparing serologically pure virus antigens. The test for purity of virus antigens is the presence or absence of a precipitin reaction with the healthy plant antiserum. If plant proteins are present in the virus antigen, the homologous antiserum will react with the juice of healthy plants used as antigen. If plant protein is not present, no precipitin reaction will be obtained. However, if the purified virus is antigenic and a precipitin reaction is obtained only with preparations containing the virus, the reaction can be logically attributed to its presence.

Experimental procedure

First, antigens were prepared from healthy tobacco plants and from mosaic (Tobacco Virus I Johnson) plants using several methods of purification; second, rabbits were immunized with these antigens; and, third, the immune sera produced were used for the precipitin ring tests. Readings of these tests were made after one and two hours' incubation at 25° C., and were confirmed after the tubes had remained in the icebox overnight.

PREPARATION OF ANTIGENS.—The five antigens used in this experiment were: healthy plant antigen,[1] crude mosaic antigen, acetone precipitate antigen, tryptic digest antigen, and tomato mosaic antigen $Al(OH)_3$.

Young healthy tobacco plants were ground in a food chopper and the juice extracted from the resulting pulp by subjecting it to 5000 pounds' pressure. The juice was then centrifuged, and the liquid passed through a Berkefeld filter and used without further treatment as healthy plant antigen.

Juice from tobacco plants that had been inoculated with mosaic virus (Tobacco Virus I Johnson) was pressed out according to the method used in preparing healthy plant antigen, and divided into three portions which were treated individually to form three kinds of virus antigens. One portion was filtered through a Berkefeld V filter and used without further treatment as crude mosaic antigen. A second portion of 500 cc. of juice was treated with lead acetate and barium hydroxide to precipitate proteins, salts, and carbohydrates, then centrifuged, and the supernatant treated with two volumes of acetone. The acetone precipitate was filtered off and taken up in 50 cc. of distilled water. This suspension is hereafter referred to as acetone precipitate antigen. According to VINSON and PETRE (**12**) this method of purification gives high concentration of relatively pure virus. The third portion of the juice was digested for 48 hours with 2 per cent trypsin, passed through a Berkefeld V filter, and used as tryptic digest antigen. Coagulated egg white was added to one tube of the mosaic plant juice and trypsin to check the activity of the trypsin.

The method of BREWER, KRAYBILL, SAMSON, and GARDNER (**2**) was followed in preparing tomato mosaic antigen $Al(OH)_3$. Tomato plants which had been inoculated with Virus I Johnson were ground in a food chopper, and the juice strained through gauze and supercentrifuged at 33,000 r.p.m. The residue was taken up in water, shaken vigorously, centrifuged, and the supernatant cleared with $Al(OH)_3$. This suspension was highly infectious, as evidenced by the number of local lesions on *Nicotiana glutinosa* (**4**). It did not give a biuret test for protein.

[1] All plants were grown in the greenhouse.

Sodium chloride was not used to extract the ground plant tissue since there is a possibility that it might increase the plant proteins in the expressed juice.

PRODUCTION OF ANTISERA.—Rabbits were immunized in duplicate with the five antigens described. Intraperitoneal injections of 5 cc. each were given every third day. A test bleeding made after the fourth injection showed no reactions with the healthy plant antigen against its homologous serum. The rabbits were then given

TABLE I

PRECIPITIN TESTS WITH HEALTHY PLANT JUICES IN PRESENCE OF HOMOLOGOUS AND HETEROLOGOUS ANTISERA

?=INDECISIVE, o=NO REACTION, +=FAINT RING, ++=SMALL BUT DEFINITE RING, +++=MODERATE RING, ++++=WIDE RING

ANTISERUM	HEALTHY PLANT ANTIGEN DILUTIONS								CONTROL NaCl
	1:1	1:2	1:4	1:8	1:16	1:32	1:64	1:128	
Healthy tobacco	+++	+++	+++	++	+	o	o	o	o
Crude mosaic	+++	+++	+++	+++	++	+	o	o	o
Tryptic digest of mosaic plant	?	?	?	o	o	o	o	o	o
Acetone precipitate of mosaic plant	?	o	o	o	o	o	o	o	o
Tomato mosaic $Al(OH)_3$	o	o	o	o	o	o	o	o	o
Control (normal rabbit)	o	o	o	o	o	o	o	o	o

three more injections of 5 cc. each, and on the sixth day after the last injection bled aseptically. The blood was allowed to clot and the immune sera collected in sterile bottles.

PRECIPITIN RING TESTS.—The sera were pipetted into small precipitin tubes and layered with the desired dilution of antigen. The tubes were incubated at 25° C. for an hour and were then examined for the presence of a ring of precipitate at the interphase between the serum and the antigen. These readings were checked after another hour's incubation. The tubes were placed in the icebox overnight and examined for precipitate the next morning. All tests were run in duplicate. Each antigen was tested with homologous and heterologous antisera. Table I illustrates the method of setting up such a test with one antigen.

Discussion

The results of preliminary experiments with crude extracts of healthy and diseased plants indicated that these materials had antigenic substances in common. (The precipitin tests are summarized in table II.) This is what is to be expected, of course, since unaltered plant protein was probably present in both types of preparation and would constitute a common antigen.

TABLE II

PRECIPITIN TESTS WITH FIVE ANTIGENS AND THEIR HOMOLOGOUS AND HETEROLOGOUS ANTISERA

o = NO REACTION, + = DEFINITE PRECIPITATE

Antiserum (undiluted)	Antigen (dilution 1:4)						
	Healthy tobacco plant	Crude tobacco mosaic plant	Acetone precipitate tobacco mosaic virus	$Al(OH)_3$ purified tomato mosaic virus	Tryptic digest of tobacco mosaic plant	Control 2% trypsin*	Control NaCl
Healthy plant	+	+	o	o	o	o	o
Crude tobacco mosaic	+	+	+	+	+	o	o
Acetone precipitate tobacco mosaic virus	o	+	+	+	+	o	o
$Al(OH)_3$ purified tomato mosaic virus	o	+	+	+	+	o	o
Tryptic digest of tobacco mosaic plant	o	+	+	+	+	+	o
Normal rabbit serum (control)	o	o	o	o	o	o	o

* Trypsin is antigenic and gives a precipitin test with tryptic digest antisera. However, this does not invalidate the results of the precipitin tests with other antigens.

Further experiments, summarized in table II, showed also that crude extracts of mosaic-diseased plants and purified preparations of virus from such extracts also had common antigenic factors. It might be expected that this would prove to be the case, but here the question arises as to whether the common antigenic substance or substances were (1) unmodified plant protein present in the crude extract and not entirely removed by the different methods of purification employed; (2) antigenically altered plant protein; or (3) the virus, *per se*, present in both crude and purified preparations.

Experiments were conducted in which antisera were prepared for virus material purified by the three methods already described. The precipitin tests, utilizing crude juice of healthy plants as an antigen in addition to the virus preparations, indicated that the purified virus preparations contained a common antigenic factor which was not present in the juice of healthy plants. This fact is of particular significance from two points of view. First, the methods of virus purification employed eliminate all or practically all unmodified plant proteins which may serve as antigens; second, the antigenic substance which gives rise to positive reactions with these antisera is not present in healthy plants.

The possibility that the common factor present in crude and purified preparations of virus is antigenically altered plant protein must be considered. However, inasmuch as virus purified by acetone precipitation and by tryptic digestion from tobacco as well as virus purified by $Al(OH)_3$ adsorption from tomato were used as antigens, it seems improbable that the antigenic factor common to the purified preparations was antigenically altered plant protein.

Filtration experiments

During filtration experiments with Tobacco Virus I Johnson, it was noticed that the Seitz E. K. filter[2] removed virus, and that the filtrate was not infectious until several hundred cubic centimeters of juice had passed the filter. Since the virus was held back by the filter while most of the plant protein had passed through, it would seem that if the precipitin reaction is due to altered plant protein, the Seitz filtrate should give a precipitin test, unless the virus alters the protein so that it is not filterable. However, if the positive precipitin test is due to the virus, no reaction would be expected.

An experiment was conducted to test this hypothesis. Juice from mosaic tobacco plants was cleared by filtration through a Berkefeld V filter and divided into three portions, one of which was used without further treatment as crude virus I antigen. The second portion was filtered through a Seitz filter and used as antigen crude Seitz filtrate. The third was treated with $Al(OH)_3$, according to the method of Brewer et al., to remove the plant proteins, and again divided

[2] The Seitz filters used were of 100 cc. capacity. Two pads were used.

into two portions. One part was filtered through a Berkefeld V filter and used as antigen $Al(OH)_3$ Berkefeld filtrate; this filtrate was infectious. The other was passed through a Seitz filter and used as antigen $Al(OH)_3$ Seitz filtrate; it was not infectious.

The antiserum used was obtained from a rabbit immunized with a purified preparation of tobacco mosaic virus from tomato.

The results given in table III tend to confirm the hypothesis that the precipitin reaction depends upon the presence of the virus, since

TABLE III

EFFECT OF SEITZ FILTRATION ON PRECIPITIN REACTION OF SELECTED ANTIGENS

o = NO REACTION, + = DEFINITE PRECIPITATE

ANTISERUM (DILUTION 1:4)	ANTIGENS (DILUTION 1:2)				
	CRUDE MOSAIC	SEITZ FILTRATE OF CRUDE MOSAIC	TOBACCO MOSAIC $Al(OH)_3$ BERKEFELD FILTRATE	TOBACCO MOSAIC $Al(OH)_3$ SEITZ FILTRATE	HEALTHY PLANT
Crude mosaic virus I....	+	+	+	o	+
$Al(OH)_3$ tobacco mosaic..	+	o	+	o	o
Healthy plant.....	+	+	o	o	+

the purified virus antiserum reacts with crude or purified antigens which contain the virus but not with the Seitz filtrates of purified virus which do not contain the virus. Seitz filtrates of crude virus juice react with the healthy plant antiserum, indicating that the plant protein passes the filter.

RESULTS OF PRECIPITIN TESTS

1. Crude extracts of healthy and mosaic-diseased tobacco plants have antigenic substances in common.

2. Crude extracts of mosaic-diseased plants and purified preparations of the crude extracts have antigenic substances in common.

3. Antisera prepared for the virus purified by three different methods show a common factor which appears to consist of the virus, or a complex containing the virus, since the antisera reacted with

crude virus-containing plant juice but not with the crude juice of healthy plants.

4. Purified preparations of tobacco mosaic virus from tomato plants reacted with antisera for crude virus-containing juice from tobacco plants and with the antisera for purified preparations, but not with juice from healthy tobacco plants, indicating that the reactions secured were due to the virus and not to the plant protein.

5. Berkefeld filtrates of purified virus were infectious and reacted with the antisera prepared against virus-containing antigens.

6. Seitz filtrates of crude virus were not infectious and did not react with the antisera prepared for the purified virus, but did react with the crude mosaic antiserum and with healthy plant antiserum.

The results of PURDY and of MATSUMATO and SOMAWAZA on the virus of tobacco mosaic are thus confirmed. In addition, evidence has been obtained that the precipitin reactions secured are specific for the virus, or a complex containing the virus, since similar results are obtained regardless of the method employed in purification of the virus.

Part II

PROBLEM

An attempt was made to differentiate several plant viruses by the precipitin test. The viruses[3] used were: spot necrosis (Tobacco Virus IV Johnson), ring spot (Tobacco Virus V Johnson), tobacco mosaic (Tobacco Virus I Johnson), and attenuated forms of spot necrosis and tobacco mosaic (**5**).

EXPERIMENTAL PROCEDURE

It was soon discovered that the various methods used for purification of tobacco mosaic are not adequate for purification of other viruses, so that considerable experimentation on methods of purification was necessary. In the preparation of antigens of spot necrosis, ring spot, and attenuated spot necrosis, precipitation of the virus with safranin and removal of the safranin by adsorption with Lloyd's reagent according to the method described by VINSON (**11**) proved most satisfactory.

[3] Professor JAMES JOHNSON of the Department of Horticulture, University of Wisconsin, kindly supplied the pure strains of the viruses used in this study.

PURIFICATION BY SEITZ FILTER METHOD.—The antigen of Tobacco Virus I was purified and concentrated by adsorption on a Seitz filter and subsequent elution with buffers. Since this method has not been reported previously it is described here in detail. Adsorption of the virus of tobacco mosaic by the Seitz filter, already noted, had suggested the possibility of using it to collect, purify, and concentrate the virus. Accordingly diseased plants were ground in a food chopper, the crushed material frozen and thawed, and the juice pressed out and centrifuged until clear. The supernatant fluid (the crude plant juice) was first passed through a Berkefeld V filter to remove materials not precipitated by centrifuging, and then passed through a Seitz filter. To remove the accumulated plant material from the pad, the Seitz filter was washed with about 200 cc. of distilled water, or until the filtrate was clear and colorless. Experiments on the infectivity of the filtrate show that distilled water does not remove the adsorbed virus from the pad to any appreciable extent.

Filtration is a complex phenomenon and many factors other than pore size are involved. Perhaps the two most important factors determining the filterability of particles are (1) the charge of the particle and of the filter, and (2) the surface tension and the pH of the menstrum. In order to determine which of these factors caused Tobacco Virus I to be adsorbed on the Seitz filter pad, three methods of releasing it were employed: electrophoresis, use of surface tension depressants, and change of pH with buffers.

If the viruses are adsorbed on the Seitz filter because of a difference in the charge of the virus (1) and the filter, it would seem possible to suspend the adsorbed virus in an electrolyte and to release it by electrophoresis. Consequently Seitz filter pads through which 500 cc. of mosaic juice had been passed were ground in 50 cc. of 0.85 per cent NaCl solution. This suspension was placed in a U-tube and electrodes carrying 110 volts of direct current introduced. Samples of the suspension were removed from both poles at 2-, 4-, and 20-hour intervals. The samples from the negative pole contained no virus and those from the positive pole only a small amount, as evidenced by their infectivity when tested by HOLMES'S method. The experiment was repeated on the other viruses with

similar results. It is possible that the virus may have been inactivated or killed by the concentration of chlorine liberated during electrolysis.

Since electrophoresis did not effectively separate the virus from the filter, ethyl alcohol, as a surface tension depressant, was next tried. After filtering 500 cc. of Tobacco Virus I, the Seitz filter was washed alternately with 40 cc. of 95 per cent ethyl alcohol and 10 cc. of water until a total of 100 cc. of liquid had been passed through it. The alcohol was removed from the filtrate by distillation *in vacuo* at 40° C., and the remaining suspension diluted to 500 cc. and tested for infectivity on *Nicotiana glutinosa*. The three plants inoculated with crude untreated juice showed an average of eighteen lesions per leaf, while the three plants inoculated with the alcohol-free filtrate showed an average of forty-five lesions per leaf, thus indicating a relatively high concentration of virus.[4] The experiment was repeated using methyl alcohol with essentially the same results. The method seems to offer possibilities for the purification and concentration of Tobacco Virus I, which is very resistant to alcohol. However, when the experiment was repeated with spot necrosis, attenuated spot necrosis, and ring spot, the viruses were evidently inactivated or killed by the alcohol.

Finally, elution of the viruses was attempted by the use of SÖRENSEN'S phosphate buffers at pH 6.0, 6.3, 6.6, 7.0, 7.2, 7.6, and 8.2. It seemed probable that since adsorption depends to some extent upon pH, the virus might be released from the filter by the use of buffers. Two hundred cc. of crude mosaic juice was passed through a Seitz filter. The filter was washed with distilled water until the filtrate was clear and colorless, the pads were removed and macerated in 70 cc. of the buffer, and placed in the icebox overnight. This last step was not essential. The pulp was then separated from the virus suspension by filtration through a Gooch asbestos filter. While the results were not always consistent, buffers with a pH of 6.6–7.2 seemed most effective in eluting the virus. Suspensions

[4] The apparent increase of the virus obtained might be explained on the assumption that the infectious agent exists as aggregates, or is adsorbed on particles that exist as aggregates which are broken up during manipulation.

thus obtained were colorless but slightly opalescent. That they contain a high concentration of virus, as tested by HOLMES'S *Nicotiana glutinosa* method, is indicated by the following protocol.

INOCULUM	AVERAGE NUMBER OF LESIONS ON N. GLUTINOSA
Crude virus	16
Virus purified by the Seitz filter method at pH 7 and diluted to 200 cc	69
Seitz filtrate	4

It will be noted that the Seitz filtrate was slightly infectious. After filtering large amounts of virus, the Seitz filter becomes saturated and some virus passes it, although there seems to be great

TABLE IV

PRECIPITIN TESTS WITH TOBACCO VIRUS I ANTISERA AND PURIFIED HOMOLOGOUS AND HETEROLOGOUS ANTIGENS

?=INDECISIVE, o=NO REACTION, +=FAINT PRECIPITATE, ++=SLIGHT BUT DEFINITE PRECIPITATE, +++=MODERATE PRECIPITATE, ++++=HEAVY PRECIPITATE

(READINGS WERE MADE AFTER 8 AND 24 HOURS. INCUBATION, 8 HOURS AT 37° C., 16 HOURS AT ICEBOX TEMPERATURE)

PURIFIED ANTIGENS	ANTISERUM TOBACCO VIRUS I PURIFIED BY SEITZ FILTER METHOD							CONTROLS	
	DILUTIONS							NaCl	NORMAL SERUM
	1:2	1:4	1:8	1:16	1:32	1:64	1:128		
Tobacco Virus I Seitz filter method	++++	++++	++	++	o	o	o	o	o
Spot necrosis Vinson's method	o	o	o	o	o	o	o	o	o
Attenuated spot necrosis Vinson's method	?	o	o	o	o	o	o	o	o
Healthy plant Vinson's method	o	o	o	o	o	o	o	o	o
Ring spot Vinson's method	o	o	o	o	o	o	o	o	o

variation in the ease with which this is accomplished. In general the juice from old plants or from plants showing severe symptoms is more effective in saturating the filter than is the juice from young

actively growing plants. Furthermore, if the filter is saturated with paraffin oil, the virus will readily pass it.

This method of purification by adsorption of the virus on the Seitz filter and subsequent elution by the use of buffers, hereafter

TABLE V

PRECIPITIN TESTS WITH SPOT NECROSIS ANTISERUM AND PURIFIED HOMOLOGOUS AND HETEROLOGOUS ANTIGENS

o = NO REACTION, + = FAINT PRECIPITATE, ++ = SLIGHT BUT DEFINITE PRECIPITATE, +++ = MODERATE PRECIPITATE, ++++ = HEAVY PRECIPITATE

Purified antigens	Antiserum spot necrosis							Controls	
	Dilutions							NaCl	Normal serum
	1:2	1:4	1:8	1:16	1:32	1:64	1:128		
Spot necrosis Vinson's method	++++	++++	++++	++++	++++	+++	+++	+	o
Attenuated spot necrosis Vinson's method	++	++	++	+	+	+	+	o	o
Healthy plant	o	o	o	o	o	o	o	o	o
Tobacco Virus I Seitz filter method	o	o	o	o	o	o	o	o	o
Ring spot Vinson's method	++	++	++	++	o	o	o	o	o

designated as the Seitz filter method, was used in preparing Tobacco Virus I; and in a later experiment, in purifying cucumber mosaic. It has several advantages: it is simple and rapid, and does not involve the use of chemicals harmful to the virus.

PRODUCTION OF ANTISERA.—The antigens of Tobacco Virus I, purified according to the Seitz method; of spot necrosis, attenuated spot necrosis, and ring spot, purified according to VINSON'S method; and of a healthy plant were given to rabbits in a series of eleven injections of 3 cc. each. On the sixth day after the last injection the rabbits were exsanguinated, the blood allowed to clot, and the sera collected.

PRECIPITIN TESTS.—Precipitin ring tests were set up with homologous and heterologous antigens. The results were not satisfactory as the titres were too low. This was attributed to the fact that the antigens were not concentrated enough to allow dilution.

Regular precipitin tests were then run. In this case the dilutions of antigen were held constant and those of the antisera varied. The

TABLE VI

PRECIPITIN TESTS WITH ATTENUATED SPOT NECROSIS ANTISERUM AND PURIFIED HOMOLOGOUS AND HETEROLOGOUS ANTIGENS

o = NO REACTION, + = FAINT PRECIPITATE, ++ = SMALL BUT DEFINITE PRECIPITATE, +++ = MODERATE PRECIPITATE, ++++ = HEAVY PRECIPITATE

PURIFIED ANTIGENS	ANTISERUM ATTENUATED SPOT NECROSIS							CONTROLS	
	DILUTIONS							NaCl	NORMAL SERUM
	1:2	1:4	1:8	1:16	1:32	1:64	1:128		
Attenuated spot necrosis Vinson's method....	++++	++++	++++	++++	+++	++	++	o	o
Spot necrosis Vinson's method....	++++	++++	++++	+++	++	+	+	o	o
Ring spot Vinson's method.....	++	++	++	++	o	o	o	o	o
Tobacco Virus I Seitz filter method....	o	o	o	o	o	o	o	o	o
Healthy plant	o	o	o	o	o	o	o	o	o

sera were diluted with 0.85 per cent NaCl. Each precipitin tube contained 0.5 cc. of serum and 0.5 cc. of antigen.

Table IV shows that antisera for Tobacco Virus I, purified according to the Seitz method, reacts with its homologous antigen but not with antigens of the other viruses nor with the antigen of a healthy plant. This indicates that there is no serological relationship between Tobacco Virus I and the other viruses, and that the normal plant antigen had been removed by the purification methods employed.

Tables V, VI, and VII show (1) that the purified preparations of

spot necrosis, attenuated spot necrosis, and ring spot are antigenic; (2) that these viruses are not related serologically to Tobacco Virus I; and (3) that there appears to be a serological relationship between the viruses of ring spot and of spot necrosis. No significant serological difference is evidenced between spot necrosis and attenuated spot necrosis.

TABLE VII

PRECIPITIN TESTS WITH HEALTHY TOBACCO ANTISERUM AND HOMOLOGOUS AND PURIFIED HETEROLOGOUS ANTIGENS

Purified antigens	Antiserum Healthy tobacco plant							Controls	
	Dilutions							NaCl	Normal serum
	1:2	1:4	1:8	1:16	1:32	1:64	1:128		
Healthy plant.	++++	++++	++++	++++	++	++	?	o	o
Tobacco Virus I Seitz filter method.....	o	o	o	o	o	o	o	o	o
Spot necrosis Vinson's method.....	++	++	o	o	o	o	o	o	o
Attenuated spot necrosis Vinson's method.....	++	++	o	o	o	o	o	o	o
Ring spot Vinson's method	o	o	o	o	o	o	o	o	o

PRECIPITIN ABSORPTION TESTS

In order to check further the results of precipitin tests with purified antigens, precipitin absorption tests were run on the antisera prepared against the following antigens:

1. Tobacco mosaic Virus I, purified by the Seitz filter method.
2. Tobacco mosaic Virus I, crude.
3. Attenuated tobacco mosaic, Virus I, attenuated by growing plants at a high temperature.
4. Spot necrosis.
5. Ring spot.[5]
6. Cucumber mosaic, purified by the Seitz method.

[5] This strain was obtained from Dr. R. G. HENDERSON of the Department of Plant Pathology, Virginia Agricultural Experiment Station, Blacksburg.

7. Crude cucumber juice, cleared by supercentrifuging at 33,000 r.p.m.
8. Healthy tobacco plant, cleared by passing through Berkefeld V filters.

TABLE VIII

SUMMARY OF PRECIPITIN TESTS WITH ABSORBED SERA IN THE PRESENCE OF HOMOLOGOUS AND HETEROLOGOUS ANTIGENS

o = NO PRECIPITATE, + = SLIGHT PRECIPITATE, ++ = DEFINITE PRECIPITATE, +++ = MODERATE PRECIPITATE, ++++ = HEAVY PRECIPITATE

ANTIGENS (DILUTION 1:3)	TUBES	ANTISERA (DILUTION 1:10)							
		TOBACCO VIRUS I, SEITZ FILTER METHOD	VIRUS I, CRUDE	ATTENUATED MOSAIC	SPOT NECROSIS	RING SPOT	CUCUMBER MOSAIC, FILTER METHOD	CUCUMBER MOSAIC, CRUDE	HEALTHY TOBACCO PLANT
Tobacco Virus I, Seitz filter method	1	++++	++++	+++	o	o	o	o	o
	2	++++	++++	+++	o	o	o	o	o
Tobacco Virus I, crude	1	++	++	++	o	o	o	o	o
	2	+++	++	++	o	o	o	o	o
Attenuated mosaic	1	+++	++	+++	o	o	o	o	o
	2	++	++	+++	o	o	o	o	o
Spot necrosis	1	o	o	o	+	o	o	o	o
	2	o	o	o	+	o	o	o	o
Ring spot	1	o	o	o	o	o	o	o	o
	2	o	o	o	o	o	o	o	o
Cucumber mosaic, Seitz filter method	1	o	o	o	o	o	+	++	o
	2	o	o	o	o	o	+	++	o
Cucumber mosaic, crude	1	o	o	o	o	o	+	+	o
	2	o	o	o	o	o	+	+	o
Healthy tobacco plant	1	o	o	o	o	o	o	o	+++
	2	o	o	o	o	o	o	o	+++

Rabbits were immunized as previously described to each of these antigens. The antisera thus produced were absorbed with healthy plant antigen as follows. One and five-tenths cc. of a healthy plant was added to 3 cc. of each antiserum, the mixture incubated at 37° C. for four hours, placed in an icebox overnight, and centrifuged. The

supernatant liquid was pipetted into sterile test tubes and 1.5 cc. of healthy plant antigen was again added. This process of absorption was repeated until no precipitate formed upon the further addition of healthy plant antigen.

Precipitin tests

The absorbed antisera were then tested for precipitins with homologous and heterologous antigens. Five-tenths of a cubic centimeter of 1:10 dilution of antiserum was added to 0.5 cc. of 1:3 dilution of antigen. These dilutions of antigen and antiserum were employed because preliminary experiments had shown that if cross-reactions occurred, they were most likely to appear under these conditions.

The results of these tests, summarized in table VIII, indicate that when precipitins of a healthy plant have been removed from the antiserum by absorption with healthy plant antigen, the serum gives a positive test only with the homologous virus antigen. This confirms the results of tests with purified antigens. No difference could be detected between Tobacco Virus I and an attenuated form. The absorbed ring spot antiserum did not give any reaction with homologous or heterologous antigen. The titre of the ring spot antisera with homologous antigen was 1:8, consequently the dilution that resulted when the serum was absorbed was too great to give a reaction.

Summary

1. The juice from virus-diseased plants contains, in addition to the antigenic constituents of a normal healthy plant, an antigenic fraction which, by the methods employed, is inseparable from the virus itself. This holds true in the case of Tobacco Virus I whether the virus is grown in tobacco or in tomato. This antigenic factor not only accompanies the virus but is specific for a particular virus, in that the antibodies induced by one virus are qualitatively different from those induced by other viruses.

2. Viruses may be freed from the antigenic constituents of healthy plants by several methods of purification. A new method by use of a Seitz filter is described. Regardless of the method of purification, however, it was not possible to separate the virus, as judged by infectivity, from the specific antigenic factor which accompanies it.

3. Close association of the antigenic factor with infectivity and

the specific nature of the antigenic fractions accompanying the different viruses strongly suggest that this specific antigenic factor is either the virus itself or a virus-plant-protein complex in which the virus plays the rôle of a haptene. Whatever the true explanation of the nature of the specificity of the reaction may be, the reaction seems to be specific for the virus. The precipitin test should prove to be a valuable aid in the further classification of plant viruses.

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AMMONIUM AND NITRATE NUTRITION OF DORMANT DELICIOUS APPLE TREES AT 48° F.[1]

G. T. NIGHTINGALE

Introduction

In previous publications (**6, 7, 8, 9**) it has been repeatedly pointed out that plants may absorb large quantities of nitrate nitrogen; but unless nitrates first combine with carbohydrate materials to form proteinaceous compounds, there is little apparent effect upon the growth of the plant. Recent work by TIEDJENS (**18, 19, 20**) has also indicated that absorption of ammonium nitrogen by plants does not result in the formation of new cells and growth unless followed by the assimilation or synthesis of the ammonium nutrient to organic compounds of nitrogen.

In the process of protein synthesis from nitrates, there are found in the plant in successive stages nitrites and ammonium nitrogen (**1**). Obviously, on a theoretical basis, ammonium compounds should therefore be more rapidly assimilated by the plant than nitrate containing nutrients. TIEDJENS (**18, 20**) has demonstrated that, for Delicious apple trees in sand culture under usual greenhouse temperature conditions, the most favorable initial pH of the nutrient solution, for assimilation of the nitrate ion was about 4.5, and for the ammonium ion about 6.0.

THOMAS (**16**) and ECKERSON (**2**) have demonstrated that in apple trees the fine fibrous roots are the organs chiefly responsible for the initial stages in protein synthesis. It is a fairly common practice in some fruit growing sections to apply nitrogenous fertilizers to the orchard in the early spring, before the leaves have expanded and while soil and air temperatures are still comparatively low. With this in mind, the present work was undertaken to determine the relative rate of availability of ammonium and nitrate nitrogen in the case of

[1] Through the courtesy of the University of Chicago there was made available for this work the temperature control equipment and laboratory facilities of its Department of Botany. The writer wishes also to express his appreciation of the advice and cooperation of E. J. KRAUS and M. A. BLAKE.

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Delicious apple trees at a temperature of 48° F. This temperature, as will be shown in a later publication, probably approaches, for many varieties of apples, the lower limit of possible assimilation of nitrogenous nutrients.

Experimental methods

During the summer of 1932, about 300 specially selected 18-inch, 1-year-old Delicious apple trees, which had been root grafted on seedling roots, were grown in the greenhouse in sand culture. The trees were cut back to a uniform height of 12 inches when placed in the sand, and all buds except one were removed. For the first few weeks the trees received a complete nutrient solution, until the single shoot upon each tree had attained a growth of about 12 inches. At that time the nutrient treatment was changed, so that the trees received no external nitrogen supply but did receive all other nutrients. At the end of the summer the trees exhibited the usual symptoms of nitrogen deficiency. The foliage was light green with reddish petioles, and the bark was yellowish in color except near the terminal growing point where it was reddish yellow. The current twig growth was relatively short, of small diameter, stiff and lignified, and practically all parenchymatous tissue throughout the trees was packed with starch grains. In proportion to tops the trees had an enormous volume of very fine white fibrous roots that appeared nearly to fill the 12-liter self-draining porcelain jars in which they were grown, three trees per jar.

At the end of the summer, after all the leaves had abscissed, the crocks and trees were shifted intact to a cold storage cellar at 35°–40° F., where they remained until January 6, 1933, with no treatment other than application of tap water as required to keep the sand constantly moist. On that date the trees were removed from the crocks and the current stem cut back to two buds. All the fine fibrous roots were removed, so that there remained only old roots, none of which was less than 1 cm. in smallest diameter.

The trees were then selected for uniformity and reset in nitrogen-free white quartz sand in new 10-inch clay pots, three plants per pot. They were grown in a greenhouse at about 50° F. and received daily applications of minus-nitrogen nutrient solution (table I) in suffi-

cient amount to flush the sand of each culture. On February 12, 56 trees (hereafter referred to as initial trees) were harvested for analysis. The two buds that remained after the pruning treatment already described had expanded to the extent that leaves were visible and were about 1 cm. in length. During the same period roots had developed rapidly. The first formed new roots were from 8 to 16 cm. in length and had many laterals. The entire new fibrous root system was white and succulent with a green weight of 4.8 gm. per tree.

TABLE I

COMPOSITION OF NUTRIENT SOLUTIONS. PARTIAL VOLUME MOLECULAR CONCENTRATIONS OF SALTS USED

SERIES	pH	$Ca(NO_3)_2$	$(NH_4)_2SO_4$	$CaCl_2$	KH_2PO_4	$MgSO_4$
Minus N	5.0	.....	.....	0.0090	0.0045	0.0045
Ammonium N	6.0	.....	0.0045	0.0045	0.0045	0.0045
Nitrate N	4.5	0.0090	.....	.....	0.0045	0.0045

At the time of initial analysis the remainder of the trees were placed in continuous darkness in a cold storage room at 48° F. (±0.5). They were divided into three groups each containing 30 trees. Each group received the respective nutrient solution indicated in table I. The solutions were percolated through the sand according to the constant renewal method of SHIVE and STAHL (**15**) at the rate of 36 liters per culture every 24 hours. This rate of renewal was such that the solution, after passing through the sand, did not vary more than 0.1(±)pH from that initially supplied (table I). The same solution was passed through the sand three times daily, the necessary adjustments of the pH being made after each passage with 0.1 N KOH or H_2SO_4 as required. At the end of 24 hours the solution was replaced by nutrient not previously used. This treatment was continued for 16 days, at 48° F.

In addition, six of the trees of the ammonium sulphate group and a similar number of the calcium nitrate group were grown in water cultures instead of in sand. The solutions of this lot were also changed at the rate of 36 liters per culture per day, and in addition each water culture was vigorously stirred with a motor-driven agitator so that the new white fibrous roots were in constant gentle waving motion.

Chemical methods

Plant fractions.—The new fine fibrous roots, the analyses of which are given in table II, consisted of new roots only. They were white, very succulent, relatively young, and not more than 0.2 cm. in diameter (most of them were less). Because of the pruning treatment already described, no roots were present which were intermediate between new fibrous roots and old large roots. The old large roots, together with the wood growth of 1931 and that of 1932, are included as a single analytical sample (table II). The two buds per tree, which were slightly expanded, were analyzed as a third analytical sample; and the results of the analyses of these buds, in so far as they are pertinent, are given in the context.

Nitrogenous fractions.—The new fine fibrous roots were minced with a large knife and thoroughly mixed. Aliquots were boiled for 20 minutes (**21**), following which they were ground with a mortar and pestle and extracted. Nitrogenous fractions were determined as previously described (**10, 11**), with the single exception that ammonium nitrogen was determined by aeration of the coagulum-free extract with 6 per cent NaOH. The old large roots and tops were rapidly cut in a specially constructed mill and the resultant thin shavings were boiled and extracted in the same manner as the roots.

The term organic nitrogen is synonymous with ammonium and nitrate-free nitrogen.

The pH estimations were made colorimetrically, using as standards the colored glass discs of a Hellige Klett color comparator.

Discussion of results

During the 16-day period at 48° F. the buds expanded slightly, but made little if any measurable growth. The roots grew rapidly, however, and for the period of the experiments were essentially the same in appearance, weight, and volume under all nutrient treatments. The average green weight of new, fine fibrous roots was about 9 to 10 gm. per tree when finally harvested for analysis, as contrasted with 4.8 gm. at the time of commencing experimental treatment 16 days previously. In the water cultures the growth of individual roots was easily observed and measured, and it was found that some elongated 1–2 cm. in 24 hours. This is in striking contrast to the

TABLE II

DORMANT DELICIOUS APPLE TREES GROWN IN SAND CULTURE AT 48° F. AND CONSTANT pH VALUES
(NITROGENOUS FRACTIONS AND DRY MATTER EXPRESSED AS PERCENTAGE OF GREEN MATTER)

	NEW FINE FIBROUS ROOTS							OLD LARGE ROOTS AND TOPS						
	INITIAL	8 DAYS			16 DAYS			INITIAL	8 DAYS			16 DAYS		
	pH 5.0 MINUS N	pH 5.0 MINUS N	pH 4.5 $Ca(NO_3)_2$	pH 6.0 $(NH_4)_2SO_4$	pH 5.0 MINUS N	pH 4.5 $Ca(NO_3)_2$	pH 6.0 $(NH_4)_2SO_4$	pH 5.0 MINUS N	pH 5.0 MINUS N	pH 4.5 $Ca(NO_3)_2$	pH 6.0 $(NH_4)_2SO_4$	pH 5.0 MINUS N	pH 4.5 $Ca(NO_3)_2$	pH 6.0 $(NH_4)_2SO_4$
Dry matter	7.060	7.850	6.370	6.090	7.910	6.060	4.950	26.500	26.750	25.500	25.750	25.800	24.720	24.000
Total organic N	0.102	0.109	0.274	0.333	0.110	0.380	0.616	0.081	0.077	0.082	0.087	0.084	0.089	0.094
Protein N	0.073	0.076	0.164	0.149	0.092	0.183	0.216	0.048	0.047	0.045	0.049	0.051	0.051	0.054
Soluble organic N	0.029	0.033	0.110	0.184	0.018	0.197	0.400	0.033	0.030	0.037	0.038	0.033	0.038	0.040
Amino N	0.004	0.004	0.045	0.077	0.003	0.067	0.120	0.002	0.002	0.003	0.003	0.002	0.004	0.005
Amide N	0.003	0.004	0.021	0.040	0.002	0.049	0.076	0.002	0.002	0.002	0.003	0.001	0.003	0.003
Ammonium N	None	None	0.002	0.006	None	0.003	0.008	None	None	Trace	Trace	None	Trace	Trace
Nitrate N	None	None	0.011	None	None	0.014	None	None	None	None	None	None	None	None

extremely slow growth of the aerial organs, which grew rapidly, however, when a few of the trees were shifted to a temperature of 70° F.

The pH values selected for the ammonium and nitrate cultures (table I) were not chosen arbitrarily, but are those found by TIEDJENS (**18, 20**) to be favorable for the growth of Delicious apple trees in sand culture when the nutrient solution was maintained at a practically constant pH value. As usual (**5, 12, 13, 19**), the ammonium sulphate cultures tended to become more acid, a change which is generally considered (**13**) to be due mainly to the more rapid absorption of the ammonium than of the sulphate ion; and the calcium nitrate nutrient solutions became more alkaline owing to less absorption of the calcium than of the nitrate ion. As already pointed out, the solution of each culture constantly underwent renewal at the rate of 3 liters per hour; and as a result the solution, after passing through the sand, did not vary more than 0.1 pH from that initially supplied. Nevertheless the trees receiving the ammonium sulphate at pH 6.0 had, at the absorbing surface and tips of the fine fibrous roots, a pH of 4.0 to 4.5. The sand immediately adjacent to the roots also had about the same H-ion concentration, with a gradient reaching pH 6.0 at about 2 cm. from the absorbing surface of the root.

The calcium nitrate cultures at pH 4.5 had, at the absorbing surface and tips of the fine roots, a pH of 5.6, as did also the sand in contact with the roots; although less than 1 cm. from the roots the solution on the sand particles was about pH 4.5. On the other hand, the minus-nitrogen cultures at pH 5.0 did not noticeably affect the H-ion concentration of the solution as a whole, and the surface of the fine roots appeared to have a pH value of approximately 4.8–5.0. Yet the roots, although somewhat more slender, were growing (at least in length) at about the same rate as in the case of the trees receiving nitrogen in the nutrient solution.

Both the ammonium and the nitrate series were duplicated in water culture. The solutions which bathed the roots underwent constant renewal at the rate of 3 liters per hour and were continuously and vigorously stirred with a motor-driven agitator. Even under these conditions the ammonium sulphate (pH 6.0) cultures had at the surface of the fine absorbing roots a capillary film of pH 5.4,

while the trees supplied with calcium nitrate nutrient solution at pH 4.5 had at the surface of the absorbing roots a film of pH 5.2.

It is obviously impossible, in sand culture, absolutely to control the pH of the solution bathing the roots, if the plant is absorbing from the nitrogen-containing salt of the nutrient solution in largest part ammonium from ammonium sulphate or nitrate from calcium nitrate. Under the conditions of water culture, however, in which more extreme changes in pH at the root surfaces were eliminated, the trees were able to grow without injury and produce roots apparently healthy in every way, in a solution containing ammonium sulphate at a partial volume molecular concentration of 0.0180. This is four times as concentrated as that employed in most of the sand culture series (table I). A few of the trees in sand culture, which were subjected to this amount of ammonium sulphate at pH 6.0($\pm$0.1), produced roots which were short, stubby, and bulbous in appearance. This was due mainly to the development of the primordia of branch roots, most of which never developed sufficiently to emerge through the cortex, probably because of the extremely acid condition of the root surface and of the outer cortical cells which were about pH 2.8–3.0.

The preceding results would not indicate that a widely different pH of the nutrient medium is required for ammonium from that required for nitrate assimilation. Actually, as is shown in table II, the trees of the ammonium series assimilated nitrogen rapidly when the solution bathing the roots was pH 4.5, and those of the nitrate series when the absorbing surface of the roots was pH 5.6. Practically, under conditions of sand culture it is essential that the initial solution containing ammonium sulphate be approximately neutral (pH 6.0), and that that of a calcium nitrate culture be relatively acid (pH 4.5), in order that the absorbing root surfaces may not become extremely acid in the former case or excessively alkaline in the latter case. Actually in practice (17) there has been some indication that ammonium sulphate may be assimilated efficiently by fruit trees growing in a soil of pH 4.2, which was not high in soluble aluminum or other toxic materials. This is not surprising, however, as it is well known that the H-ion concentration under usual conditions changes slowly

in a well buffered soil. Obviously, however, it would be a short sighted policy to apply ammonium sulphate season after season to an acid soil, without liming. The soil would gradually lose in buffer capacity and increase in acidity, owing partially to the greater absorption of the ammonium than of the sulphate ion.

This change in pH of the solution at the surface of the absorbing roots explains certain phenomena observed by others working with sand cultures. While it is not actually a part of this investigation, it may be worth while to point out that TIEDJENS (**19, 20**) found that the plants of his initially acid calcium nitrate cultures frequently exhibited symptoms of iron deficiency, whereas the plants of his initially alkaline ammonium sulphate series did not. At first thought this would seem illogical as iron is relatively soluble in acid but insoluble in alkaline solution (**14**). Even though applied at pH 6.0, however, the solution bathing the roots of the ammonium sulphate trees became relatively acid, which would tend to keep iron in solution, as compared with the calcium nitrate cultures which, although supplied with solution at pH 4.5, became alkaline at the root surfaces, thereby tending to precipitate iron out of solution.

Some studies were made of the pH of the internal tissues, especially of the new white fibrous roots. The pH of the tissues apparently did not vary directly with the nutrient solution, except in the case just described where the trees in sand culture were subjected to ammonium sulphate at a partial volume molecular concentration of 0.0180, and in that case the roots were seriously injured. The pH values of comparable tissues of the roots of the ammonium sulphate series at pH 6.0 were essentially the same as those of the trees with no external nitrogen supply at pH 5.0, or those receiving calcium nitrate at a H-ion concentration of 4.5. The epidermis and outer two or three layers of cortical cells of the absorbing roots may have been slightly modified in the direction of the pH of the solution bathing the roots, but if so it was very slight and not true of the inner cortical cells.

The cortex varied in pH from 5.2 to 4.4, or even 4.2 in occasional cells, but the lower two figures were invariably associated with heavy deposition of starch (as in roots of the minus-nitrogen cultures), not with the pH of the nutrient medium. The phloem and cambium

were relatively alkaline, about pH 5.6–5.8, except in the case of the phloem rays which were about pH 4.6 when starch was present. The mature xylem tissue appeared to have a H-ion concentration of about 4.8–5.2, but in the vicinity of the cambium the recently developed xylem elements were approximately 5.6.

Limited examination of the old, large roots and tops also indicated a similar situation; the starch storing tissues were relatively acid and, as in the smaller roots, of a pH value approaching that usually considered optimum for diastatic digestion (pH 4.2). Relatively young tissues and the phloem, except in starch storing cells, were comparatively alkaline. This is not unlike the situation already described by ECKERSON (1) for tomato.

When the roots of the initial plants were examined, no asparagine was detected and all the parenchymatous tissue nearly to the root tips was packed with starch grains. As already emphasized, the apple trees of these experiments had been grown for an entire season with no external nitrogen supply. Such plants are notably high in nitrate reducing material (1) and in ability to synthesize organic nitrogen from nitrogenous nutrients (3). The apple trees of these experiments were apparently no exception, even though they were subjected to a temperature of 48° F.

Nitrate, when applied to these initial plants, was apparently absorbed instantly and remained in the fine roots exclusively. In about two days after application strong reactions for nitrite and ammonium were obtained, accompanying which there was definite etching of starch grains in the smaller roots, and a little later asparagine appeared. Nitrites were absent as usual, or present only in traces, following the first period of rapid nitrate reduction.

In the roots of the ammonium supplied plants no nitrate nor nitrite could be detected at any time, but ammonium was apparently absorbed instantly and was present in quantity only in the new fine roots. During the first two or three days little difference was observed in the starch and asparagine contents of the roots of the two complete nutrient series, but after eight days starch was practically absent from the fine roots of the ammonium supplied plants and did not again appear. Yet there was continuously an abundance of starch in comparable roots of the nitrate cultures, although very

much less than in the plants which received no external nitrogen supply.

Accompanying the almost complete disappearance of starch from the fine roots of the ammonium supplied trees, asparagine appeared in much larger quantity than could be detected in the fine roots of the trees receiving nitrate. No asparagine[2] was observed in the minus-nitrogen treated trees.

The situation observed microchemically is also in close agreement with the results of macroanalysis (table II). At the end of 16 days total organic nitrogen in the new fine roots of the ammonium supplied trees was nearly twice as high in concentration as in the fine roots of the nitrate cultures. That nitrate was also vigorously assimilated at this low temperature, however, is evident from the fact that there was at time of final harvest about three times as much organic nitrogen in the fine roots of the nitrate series as in these same organs of trees which received no external nitrogen supply. It is also notable that of this total organic nitrogen the soluble fractions accumulated in higher concentration than the more complex proteins. This is especially true in the case of the ammonium supplied trees (table II) and appears to be generally (**5, 18, 19, 20**) true of plants receiving ammonium as compared with nitrate nutrition.

TIEDJENS (**18, 20**) also analyzed the roots of dormant Delicious apple trees which had been grown in a warm greenhouse with ammonium and nitrate nutrition. Although his analytical sample of roots consisted partly of roots which were older than those of this investigation and therefore somewhat lower in concentration of nitrogen, nevertheless the results here reported are in complete harmony with his work. He likewise found that ammonium was assimilated more rapidly than nitrate, and that the starch content was less and the proportion of soluble organic nitrogen relatively high in the roots of his ammonium supplied trees.

In the synthesis of organic nitrogen from either the ammonium or

[2] It is not intended to indicate that asparagine is of greater significance than other relatively simple compounds of organic nitrogen. It may, however, furnish an index as to the rate of assimilation of ammonium and nitrate nitrogen and may be easily and positively identified (**4**). It should also be recorded that there were precipitated out in alcohol, along with the asparagine crystals, amino acids which were not identified.

the nitrate ion, it is obvious that there must be a decrease in carbohydrates. That such occurred is evident, not only from the microchemical observations already mentioned, but also from the fact that the roots of the trees receiving nitrogen were lower in percentage dry matter (table II) than those of the minus-nitrogen series, and by far the lowest in dry matter in case of the ammonium sulphate supplied trees. The latter, however, accumulated the greatest quantity of organic nitrogen.

The relatively rapid assimilation of organic nitrogen and accompanying decrease in carbohydrates of the ammonium supplied trees seems logical, for, as has been pointed out, the ammonium ion being further reduced than nitrate should theoretically be more quickly available. These experiments with apple trees at 48° F., together with TIEDJEN'S (**18, 20**) results at higher growing temperatures, indicate that this is true. His work further suggests that ammonium nitrogen may be continuously assimilated by plants as long as carbohydrate materials are available, whereas nitrate reduction or reducase activity (**1, 3**) often lessens as organic nitrogen accumulates and carbohydrates decrease.

Furthermore, there seems usually to be required for nitrate nutrition a much higher concentration of nitrogen in the form of nitrate than of ammonium nitrogen, if equal growth is to be obtained. Repeated trials (**12, 18, 19, 20**) appear to indicate that this is true. For this reason the nitrate cultures employed were purposely made higher in nitrogen than those supplied with ammonium sulphate (table I), the grams of atomic nitrogen per liter of ammonium and of nitrate solution being 0.126 and 0.252 respectively. It is not apparent why there should seemingly be required a greater concentration of nitrate nitrogen, although it is possible that a fairly high percentage of nitrate in the plant is required to furnish ammonium through nitrate reduction at a rate comparable with that made available to the plant in a culture supplied directly with ammonium nitrogen.

During the 16-day period there was no significant increase in organic nitrogen in the old large roots and tops (table II), indicating that at 48° F. there was little if any translocation of the newly synthesized organic nitrogen from the fine roots to the old roots and tops. Obviously, however, there was proteolysis (**6, 7, 8**) and subse-

quent translocation of soluble organic nitrogen from the old roots and tops, at least in the trees of the minus-nitrogen cultures; for these trees had available no external source of nitrogen, yet the new roots continually increased in volume of growth with no loss in percentage of nitrogen. This evident gain in absolute amount of organic nitrogen in the new fibrous roots (table II) was due to translocation from the old roots and tops.

There was a noticeable decrease of starch in the large roots of all the series near the point of attachment of new lateral roots. This was clearly evident in the ammonium sulphate series, somewhat less striking in the nitrate supplied group, and in the minus-nitrogen series was evidenced only by the etching of starch grains.

On a percentage basis the changes in dry matter in old roots and tops were small. It should be remembered, however, that this analytical fraction was made up in large part of old lignified tissues and that decrease in starch was observed to take place in only a small part of the sample as a whole, namely, near the new lateral roots. Large changes in percentage dry matter, in the samples consisting of old roots and tops, could therefore scarcely occur during the 16-day period of these investigations. Although the differences in dry matter are of necessity small (table II), they seem to reflect accurately the carbohydrate changes which necessarily occurred with root development and assimilation of nitrate and ammonium nitrogen.

At the end of 12 days at 48° F., when it was found that there was little or no translocation of the newly synthesized organic nitrogen to the old roots and tops, some of the trees of each series were subjected to a temperature of 70° F. while still in darkness. In 24 hours the buds had noticeably expanded and asparagine in extremely high concentration appeared in their rapidly expanding tissues. These trees were allowed to remain at 70° for four days, when they were harvested at the same time as the comparable series kept continuously at 48° F. During the four days at 70° the buds had expanded so that the leaves, including petioles, were 3–4 cm. in length, whereas the total leaf length of the plants retained at 48° was less than 2 cm.

Neither nitrate nor ammonium nitrogen was detected in the buds or shoots at either high or low temperatures. But Kjeldahl determinations indicated that their total organic nitrogen content on a

percentage basis was, for the buds or shoots of the minus-nitrogen cultures at 48° F., 0.61; for the comparable calcium nitrate group, 0.70; and for the ammonium sulphate series, 0.76. At 70° F. in the same order comparable figures were 0.66, 0.82, and 0.91. These data clearly indicate that, although there was little translocation of newly synthesized organic nitrogen from the roots to the tops at low temperature, there was comparatively rapid movement to the newly developing shoots after the plants were shifted to a temperature of 70° F.

Summary

1. Dormant 2-year-old nitrogen deficient Delicious apple trees were subjected to a constant temperature of 48° F. and continuous darkness. They were grown in sand, and the solutions of each culture underwent renewal at the rate of 36 liters every 24 hours. As a result, after passing through the sand, the solution did not vary more than 0.1 pH from that initially supplied. Trees were also grown with the same nutrient treatments but in water instead of in sand. The water cultures were not only renewed but were constantly stirred with a mechanical agitator.

2. The sole source of nitrogen for some of the trees was a complete nutrient solution containing ammonium sulphate supplied at pH 6.0; for others, calcium nitrate in complete nutrient solution at pH 4.5. Some cultures were also grown with no external nitrogen supply but with other essential elements at pH 5.0.

3. During the 16-day period of these experiments while subjected to a constant temperature of 48° F., buds expanded only slightly but there was vigorous and rapid development of roots in both the sand and the water cultures.

4. Simple proteins were synthesized in the fine fibrous roots of the nitrogen supplied trees. They accumulated apparently exclusively in these organs and were present in much higher concentrations than in the fine fibrous roots of the series grown with no nitrogen in the nutrient solution.

5. The trees which received ammonium sulphate, however, synthesized amino acids and asparagine more rapidly and in greater quantity than did the trees of the calcium nitrate cultures.

6. In the fine fibrous roots of the trees with no external nitrogen

supply carbohydrates increased, undoubtedly owing to translocation. But in those cases where ammonium and nitrate nitrogen were assimilated, there necessarily occurred considerable decrease in carbohydrates, especially in the case of the ammonium supplied trees which were synthesizing organic nitrogen more rapidly than the trees of the nitrate series.

7. On shifting to 70° F., a large part of the newly synthesized amino acids and asparagine was translocated from the fine roots to the buds, which expanded rapidly at the higher temperature.

8. Although the nutrient solutions after passing through the sand did not vary more than 0.1 pH from that initially supplied, the absorbing surfaces of the fine roots of the sand cultures supplied with ammonium sulphate at pH 6.0 were relatively acid (pH 4.2). Those of the calcium nitrate series at pH 4.5 were relatively less acid (pH 5.6). This was presumably due in each case to comparatively rapid absorption of the nitrogen containing ion, with consequent increase or decrease in acidity due respectively to the residual sulphate and calcium ions.

9. From these results it appears that there is not directly required a widely different pH value of the nutrient medium for ammonium as compared with that for nitrate assimilation, provided the absorbing surfaces of the roots are not subjected to extremely acid or alkaline conditions. Practically, however, it would be inadvisable continuously to apply ammonium sulphate to an acid soil, or sodium or calcium nitrate to a very alkaline soil.

10. In a few preliminary experiments in sand culture where higher concentrations of ammonium sulphate were used, there resulted an extremely acid condition of the root surface and outer cortical cells (pH 2.8–3.0). Associated with the acid condition of the cortex many of the root primordia failed to emerge, which resulted in roots that were stubby and bulbous in appearance.

11. In water cultures where the solutions were constantly stirred, similar pH changes occurred but they were much less extreme. Under these conditions where extreme changes in the pH at the root surfaces were eliminated, the roots grew vigorously and assimilated ammonium rapidly, even when present in concentrations four times as high as that in the regular nutrient solutions.

12. Except in the case just described in which injury occurred, the pH of the internal tissues did not vary with that of the nutrient solution. The pH values of respective tissues were essentially the same for all nutrient treatments.

13. The contents of the cells of the cortex of the fine fibrous roots varied in pH from 5.2 to 4.4, or even 4.2 in occasional cells, but the two lower figures were invariably associated with heavy deposition of starch (as in the roots of minus-nitrogen cultures), not with the pH of the nutrient medium.

14. The phloem and cambium were relatively less acid (pH 5.6–5.8) except in case of the phloem rays which were about pH 4.6 when starch was present. Mature xylem appeared to have a H-ion concentration of about 4.8–5.2.

15. Limited examination of old roots and tops also indicated that starch storing cells were relatively acid and meristematic tissues, as the cambium, comparatively alkaline.

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PENNSYLVANIAN FLORA OF ILLINOIS AS REVEALED IN COAL BALLS. I

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 451

ROY GRAHAM

(WITH PLATES VIII, IX AND TWENTY-SIX FIGURES)

Introduction

This paper is the result of studies made of fossil plants preserved in coal balls from Calhoun coal mine, Richland County, Illinois. The material was collected by Dr. A. C. NOÉ under the auspices of the Illinois State Geological Survey. The mine has now been abandoned, so that no more material can be collected there. The writer is much indebted to Dr. NOÉ, who kindly supplied the coal balls, and under whose direction the research was carried out.

The geologic horizon from which these petrifactions were obtained is about Middle Conemaugh in age, and is near the top of the Pennsylvanian strata found in Illinois.

Thin sections of the material were prepared by employing almost exclusively the cellulose peel process (3). By the use of this method, ten sections of material could easily be obtained to the millimeter, such close sections being almost essential in the study of the small strobili and seeds in order to get sections through critical structures. The numbers of the preparations, as given in this paper, refer to slides in the University of Chicago paleobotanical collections.

Description of plants

FILICALES

Notoschizaea robusta gen. et sp. nov. (preparations 549–553)

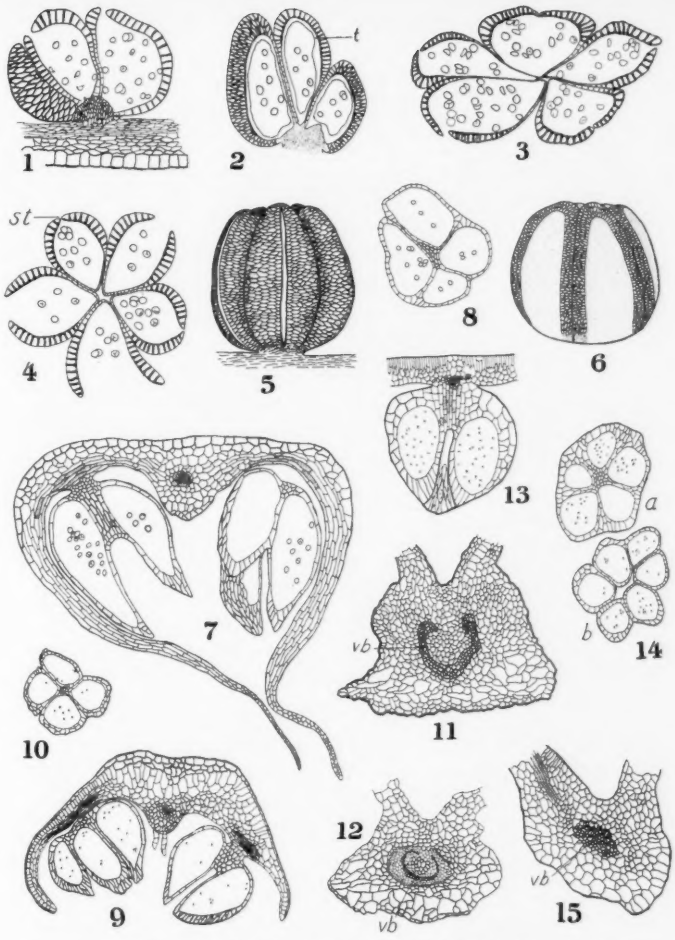
GENERIC DIAGNOSIS.—Sorus consisting of a circular group of sporangia which are so closely crowded as to resemble a synangium. Sporangia sessile, attached to the abaxial surface of a leaf by a narrow base, all of the sporangia of a sorus arising at a common point. Sporangia dehisce by means of a longitudinal cleft in the abaxial wall of the sporangium along a definite line (stomium). The outer

wall of the sporangium consists of heavy walled cells which form a wide annulus each side of the stomium.

SPECIFIC DIAGNOSIS.—Sporangia ovoid in shape, measuring about 1 mm. in length by 0.5 mm. in breadth and arranged in groups of five. Spores spherical, 55 μ in diameter, surface smooth and marked with a triradiate ridge.

This species is represented by preparations 549 to 553 in the University of Chicago collections. In preparations 551 and 552 there are excellent transverse sections of a sorus which has been slightly flattened as a result of pressure (figs. 3, 26). Five sporangia arranged in a circle make up the sorus. The sporangia are free from one another at the level of these sections but their lateral walls are flattened and in close contact. They measure about 0.5 mm. in diameter. The adjacent walls of the sporangia are thin but the outer walls are greatly thickened, measuring about 75 μ in thickness. There is a break in the continuity of the sporangium wall down the abaxial side, where dehiscence took place by means of a longitudinal cleft. On each side of this cleft the first cell (lip cell) is triangular in section, and is shorter in radial dimension than the other cells of the annulus. The apices of the triangular cells meet along the stomium. The whole of the abaxial wall of the sporangium is thus specialized to form an annulus (or more correctly, two annuli), one on each side of the stomium. The cells of the annulus are of the typical structure, with thickened inner and radial walls and a thin outer wall. Dehiscence is accomplished by the springing outward of the two annuli, thus opening a wide cleft along the stomium (fig. 4).

Preparations 552 and 553 contain obliquely longitudinal sections of the sori (figs. 1, 2). The sporangia are borne on the lower surface of a leaf and are attached thereto by means of a small common pad at their base. The sporangia are free from one another nearly to their bases. In 552 the sporangia have separated but those in 553 are closely appressed. This same state is shown in the transverse sections (figs. 3, 26) and it appears to be the normal position. In tangential section the cells of the sporangial wall are seen to be lozenge-shaped, with the long diagonal transverse to the axis of the sporangium. The cells measure about 70 by 30 μ. There appears to have been a well marked tapetum present which is preserved as a



FIGS. 1–15.—Figs. 1–5, *Notoschizaea robusta:* 1, longitudinal oblique section of sorus attached to leaf lamina (552b); 2, longitudinal but somewhat tangential section of sorus (*t*, tapetum) (553); 3, transverse section of sorus (552a); 4, same of sorus restored. Two sporangia dehiscing (*st*, stomium); 5, restoration of sorus. ×22. Fig. 6, *Coryne-pteris coralloides* (after ZEILLER) for comparison with *Sphaerotheca robusta*. ×20. Fig. 7, *Scolecopteris latifolia*, cross-section of fertile pinnule bearing sporangia. Synangium on left is in median longitudinal section. ×22. Fig. 8, cross-section of synangium of same near base. ×22. Figs. 9–12, *S. minor:* 9, cross-section of fertile pinnule (523); 10, cross-section of synangium (520); 11, 12, cross-sections of ultimate rachis (*vb*, vascular bundle) (520, 524). ×22. Figs. 13–15, *Cyathotrachus bulbaceus:* 13, longitudinal section of synangium (541); 14, cross-sections of two synangia (sectioned *a*, near base; *b*, near summit) (540); 15, cross-section of ultimate rachis (540). ×22.

dark line slightly separated from the sporangium wall (fig. 2 *t*). The structure of the leaf upon which these sporangia are borne is not well preserved, but the upper epidermis is very thick and has a palisade-like structure.

The spores are spherical and measure about 50 μ in diameter. The surface is marked by a triradiate ridge, but is otherwise smooth.

Having regard to the abaxial or dorsal dehiscence and to the robust sporangia, the name *Notoschizaea robusta* is proposed.

The individual sporangia of *Notoschizaea*, as far as the annulus is concerned, are much like those of *Etapteris*, in which there is a double, multiseriate, vertical annulus. The sporangia, however, are grouped in a circle in such a way as to resemble the synangium of *Scolecopteris* and related genera. *Notoschizaea*, like *Corynepteris*, combines characters of the Marattiaceae with those of the Zygopteridaceae. The resemblance to *Corynepteris* is very strong, and if the annuli of a *Corynepteris* were widened so as to occupy the whole of the abaxial surface of the sporangia, and the place of dehiscence changed from the ventral surface to the line of contact between the annuli, the resultant structure would be exactly as in *Notoschizaea* (figs. 5, 6). *Notoschizaea* is therefore placed provisionally with *Corynepteris* in the Zygopteridaceae.

Scolecopteris latifolia sp. nov. (preparations 542–544)

DIAGNOSIS.—Sporangia three to four borne in pedicellate circular synangia; united laterally and attached to a central column for about half their length, free above. Outer wall of sporangium not thicker than the lateral walls. Sporangia 1.1 mm. long by 3.5 mm. in diameter. Spores 35 μ in diameter. Leaves very broad and revolute, completely inclosing the sporangia.

The sporangia are borne in circular sori, three or four to a sorus. The sori are attached above lateral veins in a double series, one row each side of the midrib. The sori are pedicellate, the sporangia of a single sorus being attached to the pinnule by a common stalk which extends up the center of the sorus for nearly half the length of the sporangia. The sporangia are attached by their inner margins to this central column. Above the column they are free from one another (figs. 7, 27).

In shape the sporangia of *Scolecopteris latifolia* are ovate with a pointed end. In cross-section they are circular, except for the flattening where two sporangia are in contact (fig. 8). They measure about 1.1 mm. in length by 0.3–0.35 mm. in diameter. They are exannulate, and the sporangial walls are all of approximately the same thickness, about 20 μ, the outer wall not being thicker than the adjacent walls as is the case in *S. elegans* and *S. minor*. The walls consist of a single layer of platelike cells which are elongated in the direction of the axis of the sporangium. Dehiscence is by a longitudinal slit along the inner margin of the sporangium. The spores are much larger than those of either of the species previously described, being about 31 μ in diameter. Apart from the triradiate markings due to formation in tetrads, there are no special surface markings.

The sporangia are attached to the abaxial surface of leaf laminae. The pinnule is much revolute, the two margins almost meeting so as to inclose the sporangia. The pinnule if unrolled would measure about 7 mm. wide. The structure of the lamina of the leaf is poorly preserved, but from the various sections portions of all regions of the leaf may be made out. There is a thick upper epidermis and a rather thin and often indistinct lower epidermis, in which, however, stomata have been recognized. The mesophyll is without a distinct palisade layer. Between the point of attachment of the sporangia and the margin of the pinnule, the mesophyll consists of flattened platelike cells. The vascular bundle of the midrib consists of a small circular bundle of tracheids surrounded by a narrow zone of disintegrated parenchyma, probably in part phloem. In the lamina below each sporangium is a mass of transfusion tissue (fig. 7). This is probably part of a lateral vein. No transfusion tissue occurs in the column which supports the sporangia.

The sporangia of this species have the characters of those of the genus, but this species is very distinct from the two hitherto described. In general size of the sporangia it resembles *S. elegans* but is slightly larger. It differs from both *S. elegans* and *S. minor* in the relatively greater development of the central column, in the lack of thickening of the outer wall of the sporangia, and in the larger spores. The greater breadth of the leaf lamina is also a feature. In the development of the central column it resembles *Acitheca*, from which it

differs in having pedicellate synangia and in the absence of the bristle-like acuminate tips to the sporangia.

On account of the broad lamina of the pinnule the name *Scolecopteris latifolia* is proposed for this species.

Scolecopteris minor Hoskins.

Fronds of the *Pecopteris* type, bearing shortly pedicellate circular sori on the lower surface of the pinnule in a double series, one row on each side of the mid-vein. Pinnules measure about 2.8 mm. long by 1.7 mm. wide. Sori are circular, composed of four or five exannulate sporangia attached to the short pedicel by their inferior-basal margins. Sporangia ovate, roughly circular in cross-section with adjacent sides slightly flattened; distal ends extended into slightly concrescent acute apices by the elongation of the sporangial wall cells. Sporangia about 0.24 mm. in diameter by 0.57 mm. in length. Wall cells of the free surface much larger with heavier walls than those of the adjacent cells. Dehiscence occurs by means of a vertical cleft on the innermost wall of the sporangium. The spores are about 18 μ in diameter. The vascular bundle of the ultimate rachis is U-shaped with the ends of the arms slightly but abruptly involute (figs. 11, 32).

From several different coal balls, sections were obtained which give the structure of the ultimate rachis of a fernlike frond with pinnules bearing fructifications. The best of the material was obtained from two coal balls, C 210 and C 211B. The fern is so similar to that described by HOSKINS (**5**) as to leave little doubt as to its specific identity. There are, however, three minor differences from HOSKINS' material:

1. The pinnules are of smaller size, measuring only 2.8 mm. in length by 1.7 mm. in breadth, instead of 6–7 mm. in length by 3.3 mm. in breadth.

2. There is a well developed palisade layer in the leaf; HOSKINS' specimens had but poorly developed palisade tissue.

3. There is a wide variation in the structure of the ultimate rachis. One form (fig. 12) has a comparative weak vascular bundle surrounded by a zone of extremely thin walled parenchyma. At the other extreme the vascular bundle is much more robust and is not

surrounded by tissue different in any respect from the rest of the cortex (fig. 11). It is only the first type that HOSKINS described and figured.

These differences are modifications in vegetative structures, of the sort easily induced by environmental and other factors, and as such are not trustworthy criteria for building up taxonomic distinctions. The structural differences under (1) and (2) are possibly due to differences between a shaded environment in the case of HOSKINS' specimens and an exposed environment in the case of the specimens studied by the writer. The differences described under (3) may be due to the variation in the plane of the section. A rachis sectioned nearer the base will naturally show a larger vascular bundle and may also have other structural differences.

Cyathotrachus bulbaceus sp. nov. (preparations 535–541)

DIAGNOSIS.—Sporangia four to six, attached basi-laterally to a short central column, their bases completely united to form a saucer-shaped receptacle. The sporangia are united laterally for the greater part of their length by a common wall, a deep cup being left at the summit of the synangium. Synangia pedicellate and bulblike in shape, measuring about 0.65 mm. in diameter. Spores are 18 μ in diameter.

Preparations 535 to 541 contain sporangia attached to the under surface of a leaf lamina. There are longitudinal and transverse sections of the sporangia and obliquely transverse sections of the ultimate rachis. The sporangia are united into circular synangia similar to those of *Ptychocarpus*, but differing from that genus in several important respects.

The synangia are stalked, and each consists of from four to six sporangia united laterally at their bases to a short column which extends for about one-third the length of the sporangia, and also by a common envelope similar to but less highly developed than in *Ptychocarpus*. The uppermost parts of the sporangia are free although closely appressed (fig. 14 *b*); but nearer the base they are completely fused, the individual sporangium walls being completely merged into the common wall (fig. 14 *a*).

The sporangia are round in cross-section but are somewhat flat-

tened on their adjacent walls. In longitudinal section they are ovate in outline, with bluntly pointed tips (fig. 13). There is no annulus, but the cells of the outer wall and at the tip are larger than the others. Dehiscence probably occurred along the inner margin of the sporangia, the spores being discharged into the cup-shaped space lying between the sporangia at the summit of the synangium. The sporangia measure about 0.65 mm. long by 0.3–0.35 mm. wide. The synangia average 0.65 mm. in total diameter. The spores are round, about 18 μ in diameter, and show the characteristic tetrad markings.

In cross-section the leaf is seen to consist of an upper epidermis of platelike cells, an exceptionally well developed palisade layer consisting of much elongated prismatic cells, a spongy mesophyll, and a lower epidermis in which stomata have not been recognized with certainty (fig. 13). The synangia are attached above the secondary veins of the leaf. These veins consist of several tracheids accompanied by a much larger amount of transfusion tissue. This latter also extends into the column of the synangium but does not spread into the basal receptacle.

In the ultimate rachis (fig. 15) there is a central xylem bundle whose form appears to be elliptical in shape with the long axis parallel to the plane of the frond. The position of the protoxylem points could not be distinguished, but the tracheids are smaller on the adaxial side. Surrounding the xylem bundle is a narrow zone of exceedingly thin walled parenchyma (probably phloem), and outside this is the cortex which consists of larger cells with thicker walls. The largest cells of the cortex are found on the abaxial side of the rachis.

This sporangium is obviously closely related to those of *Cyathotrachus* and *Ptychocarpus*, with which it agrees in having a common envelope to all the sporangia of a synangium. In the presence of a central cup at the summit of the synangium it resembles *Cyathotrachus altus* Watson (**13**). It differs from that species, however, in not having a tracheal cup developed in the basal receptacle. Instead of this, transfusion tissue occupies the short central column as in *Ptychocarpus*, in which, however, the column extends the full length of the sporangia. In the sporangia studied by the writer structural agreement is much closer to *Cyathotrachus*.

The name *Cyathotrachus bulbaceus* is proposed for the species on account of the bulblike shape of the individual synangia. The absence of the tracheal cup, however, may possibly warrant its generic separation from *Cyathotrachus*.

Relationships of the Asterotheceae

Stur (**12**), in his classification of Culm and Carboniferous ferns, grouped into the suborder Asterotheceae all those forms which he considered to be of Marattiaceous affinities, those in which the sporangia of a sorus are grown together into a more or less globular synangium. The suborder included four genera: *Asterotheca* Presl, *Scolecopteris* Zenker, *Sturiella* Weiss (*Renaultia* Stur), and *Ptychocarpus* Weiss (*Diplazites* Goepp.). To these four there must now be added two others. Practically all paleobotanists have placed the fructifications of *Pecopteris polymorpha* in the genus *Scolecopteris*, although Schimper (**10**) in 1890 founded the genus *Acitheca* for its reception. In 1925 Kidston (**6**) agreed with Schimper in excluding this species from the genus *Scolecopteris*, a view which in the writer's opinion is justified on the basis of structural differences. In 1906 Watson (**13**) described isolated synangia for which he erected the genus *Cyathotrachus*. Brief descriptions of these six genera follow.

Asterotheca.—Synangia sessile, consisting of three to eight exannulate sporangia which are more or less ovate, with the free end brought to a short acute apex. The major axis of the sporangium is usually parallel to the frond which supports it. Dehiscence is by means of a longitudinal slit along the inner margin of the sporangia.

Scolecopteris.—Sporangia united laterally at their bases into a circular synangium which is shortly pedicellate. Sporangia free above, and dehiscing by a longitudinal slit along their inner margin. The long axis of the sporangia is perpendicular to the surface of the frond. The main difference between this genus and the preceding is the presence of a pedicel to the synangium.

Acitheca.—Synangia sessile, usually formed of four (rarely three or five) sporangia. Sporangia exannulate, long, rounded at base, and terminating in a sharp bristle-like point, the upper two-thirds of their length free, the basal third united to a central column. The synangia thus formed are attached by their broad bases perpendicu-

larly to the lower surface of the pinnule. The column or receptacle into which a vascular bundle extends has four plates or wings to which the sporangia are united. Dehiscence takes place through a vertical cleft along the adaxial margin of the sporangia. The margins of the pinnules are recurved and almost cover the synangia.

Sturiella.—Sporangia in groups of five, united below by their fused bases which form a concave plate attached to the pinnule by a short pedicel. The sporangia are described as cylindrical, pyriform, with adjacent sides slightly flattened (9). There is an apical annulus which caps the sporangium and runs down the dorsal wall for some distance toward the base. Dehiscence is by means of a longitudinal cleft along the inner margin of the sporangium.

Cyathotrachus.—The synangium consists of from four to seven sporangia grouped around a central receptacle which is hollowed out into a cup above. The whole is surrounded by a continuous integument. The whole structure was attached to the organ which bore it by a small base. The base apparently received a bundle from the stalk or support, and this bundle spread out into a cup of short tracheids in the sterile tissue at the base of the synangia. The sporangia probably dehisced into the central cup.

Ptychocarpus.—Sporangia almost cylindrical, contracting slightly upward with a truncate apex, attached throughout their entire length to a central column and united to each other laterally, the individual sporangia of the synangium thus formed being inclosed in a common envelope of ground tissue. The synangia are shortly stalked and each consists of from five to eight sporangia. The mode of dehiscence is unknown.

With the exception of *Cyathotrachus*, in which the pinnules are unknown, the shape of the frond in these genera is known to be of the *Pecopteris* type. The sporangia are borne in a double series, one each side of the mid-vein, the attachment of the sporangia being directly over a lateral vein.

It seems reasonable to assume that the primitive state in the Asterotheceae was that of groups of separate sporangia, each sporangium being sessile on the leaf. The fusion of individual sporangia into a synangium having a common envelope and the development of a pedicel to the synangium in all probability represent specializa-

tions. *Ptychocarpus* represents the final product of this line of evolution. The accompanying provisional family tree (fig. 38) has been drawn to show the relations among the genera.

Pteridosperms

Telangium pygmaeum sp. nov. (preparations 545–548)

Diagnosis.—Branching rachis without lamina, bearing synangia terminally or laterally on its ultimate ramifications. Synangia circular, consisting of three to five sporangia which are fused laterally for about one-third their length. Sporangia attached to the rachis by a broad base, ovoid in shape, measuring 0.6 mm. by 0.19 mm. Spores circular, 35 μ in diameter, smooth, and marked with a triradiate ridge.

Preparations 545 to 548 contain small exannulate sporangia grouped into circular synangia. These are attached to a badly preserved rachis which does not appear to be a foliage leaf (figs. 16, 30). The walls of the sporangia appear to be but one layer of cells in thickness. The sporangia are fused laterally for the basal one-third to one-half of their length. For the attachment of the terminal synangium the rachis is expanded. Other synangia are attached laterally to the same rachis by a broad area of attachment. The synangia are distinctly sessile.

Digitate clusters attached to branching petioles devoid of lamina, and associated with or attached to leaves of the *Sphenopteris* type, have been known for a great many years as plant impressions from Paleozoic rocks. These were first investigated by Stur (11) who gave to them the name *Calymmatotheca*. *C. stangeri* is the type species of the genus. Stur considered the constituent parts of the digitate clusters as indusial bracts, but Renault considered them to be sporangia.

These two conflicting opinions were held until Benson (1) obtained petrifactions of sporangia which led her to make a careful reinvestigation of Stur's type specimens of *Calymmatotheca*. She concluded that Stur's interpretation as to the nature of his specimens was correct, and that the sporangia would have to be excluded from that genus. The form genus *Telangium* with *T. scotti* as the type species was erected for these sporangia.

BENSON (1) gives the following diagnosis for the genus *Telangium:*

Fertile and barren pinnae dissimilar; fertile pinnae represented by synangia only; synangia borne at the extremity of the ultimate ramifications of the rachis, composed of six to twelve sporangia which taper to the apex and are united primarily for almost their whole length to form a body which is continued into a sterile base of decreasing diameter through which runs longitudinally a single vascular strand. Each sporange ultimately becomes almost free from the others by septicidal dehiscence and liberates large spores from a ventral suture.

One species with structure preserved, *T. scotti*, was described by BENSON. Several other species, based upon impressions only, have also been placed in this genus.

The following is a list of the previously known species:

T. scotti Benson, from the Gannister beds of Lancashire.

T. affine L. & H. and *T. bifidum* L. & H., both from the Calciferous Sandstone series of England.

T. digitatum Kidston from the Lanarkian of England.

T. nutans Carpentier from the Upper Carboniferous of France.

The fertile frond of *Sphenopteris potieri* may prove to be a *Telangium*. It is found in the Upper Carboniferous of France and also from the Staffordian of England. *T. asteroides* Lesq. has proved to be an imperfect specimen of *Crossotheca hoeningshausii*, and must therefore be dropped from the list of species of *Telangium*.

As the Illinois specimens are very much smaller than any of those previously described, the name *Telangium pygmaeum* is proposed. *T. pygmaeum* is sharply separated from the other species of *Telangium* both by its smaller size and also by the smaller number of sporangia making up a synangium. The sporangia measure only a little more than 0.5 mm. in length, whereas *T. affine*, the smallest of the previously described species, measures 2.5–3. mm., and *T. digitatum*, the largest, has a synangium composed of about 25 sporangia which attain a length of 8 mm. *T. pygmaeum* occurs considerably later in geologic time than the other species.

Conostoma platyspermum sp. nov. (preparations 501–516)

DIAGNOSIS.—Seed platyspermic, ribs absent, seed sometimes slightly 2-angled. Integument and nucellus undiverged at plinth level. Vascular strands two, in the inner region of the integument, each corresponding to an angle of the seed. Size ranges up to 4.5 mm. in length by 2.5 mm. in width by 2.0 mm. in thickness.

The genus *Conostoma* was founded by WILLIAMSON (**14**) in 1887. It included three species of small Paleozoic seeds: *C. oblongum* from the Gannister beds of the Lancashire coal fields, and *C. ovale* and *C. intermedium* from the Calciferous Sandstone series of Burntisland, Scotland. The latter two species were re-investigated by BENSON, however, who reduced them to one; and, in view of its structural differences, removed it from the genus *Conostoma* and made it the type of a new genus, *Sphaerostoma*. In 1911 OLIVER and SALISBURY (**8**), having new and more abundant material available, restudied *Conostoma*. *C. oblongum* was redescribed in greater detail, and a new species, *C. anglo-germanicum*, was founded on material from Shore, Littleborough, England, and from Duisburg in Rheinpreussen, Germany. KRICK (**7**) has also described *C. oblongum* from coal ball material from coal no. 5 at Harrisburg, Illinois.

In the study of coal ball material from Calhoun, a related but undescribed species of seed came to light. The seed is represented by a number of specimens, all found in the same coal ball, but without any organic connection between them and any other material. In view of the pronounced platyspermic nature of the seed it is proposed that the new species be called *Conostoma platyspermum*.

OLIVER and SALISBURY (**8**) give the following diagnosis of the genus *Conostoma:*

> Cylindrical or slightly flattened seeds with tapering insertion. Ribbed throughout, or at base with angles passing into ribs. Lobing at apex variable; vascular bundles equalling or fewer than the ribs or angles; loculi of canopy nearly obliterated and equalling the vascular bundles in number; epidermis mucilaginous. Lagenostome very small, included; cells of wall sculptured. Plinth conspicuous, dome shaped, with internal tissue; well marked "tent pole" and tapetum present.

The Illinois specimens agree in all essential features with this generic diagnosis, and are thus included in the genus *Conostoma*.

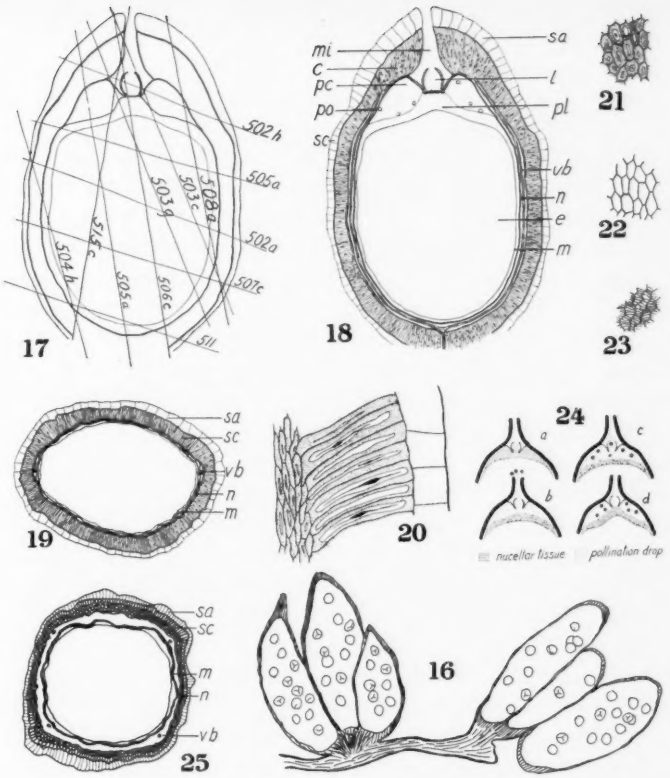
The new species differs from *Conostoma oblongum* and *C. anglo-germanicum* in being distinctly platyspermic, although *C. oblongum* in some measure shows this feature. In cross-section the seed is elliptical in outline. In all three of the specimens of which transverse sections are at hand (preparations 502, 505–512, 513) the flattening is parallel to the plane in which the two vascular bundles lie (principal plane of the seed), so that such flattening can scarcely be ascribed

to deformation of the seed (fig. 19). In longitudinal section the seed is somewhat oblong, with more or less parallel sides (figs. 18, 32, 33), but the whole structure is relatively shorter than that of *C. oblongum* and *C. anglo-germanicum*. An interior mold of the seed is shown in figure 31.

The new species has a single integument and the nucellus is undiverged to near the summit of the latter. The integument has a characteristic structure, making it easy to recognize various sections of the seed as belonging to the same species. It is composed of three distinct layers: a sarcotesta; a middle layer or sclerotesta; and an inner layer of delicate tissue, for the most part not preserved, but which must have surrounded the nucellus and in which the vascular bundles ran. In some cases the greater part of the thin sarcotesta has been lost by exfoliation, from which habit OLIVER and SALISBURY gave to it the name "blow-off" layer in their description of *C. oblongum*. The sclerotesta is variable in thickness, depending on the seed and on the plane of section. In the body of the seed its thickness is 0.1–0.23 mm. At the summit the integument becomes much thickened to form a conical canopy surrounding the micropyle.

The nucellus measures about three-fourths the length of the seed. It is non-diverged from the integument for its whole length (fig. 18). At the summit there is a large pit or depression, from the floor of which the small lagenostome arises. The lower portion of the nucellus is replaced by the growth of the megagametophyte (endosperm), the megaspore membrane marking the contact of the two structures. Only faint and indefinite traces of nucellar and megagametophyte tissues are preserved, excepting the tapetal layer of the nucellus surrounding the latter. The part of the nucellus above the megagametophyte is known as the plinth. The summit of the plinth is occupied by a plinth cavity which functioned as a pollen chamber.

The hard part of the testa which gives the shape to the seed is elliptical in cross-section, cylindrical, and tapering with a steep curve toward the micropyle, and curving more sharply to the chalaza at the other. Thus the longitudinal section of the seed has the characteristic boat shape of *Conostoma*, the micropylar end representing the prow and the chalaza the stern. The length of the seed varies from 1.6 to 2.6 mm. in the measured longitudinal sections; but if the seed



FIGS. 16–25.—Fig. 16, *Telangium pygmaeum:* two synangia attached to a rachis (546). ×44. Figs. 17–24, *Conostoma platyspermum:* 17, diagrammatic sketch of median longitudinal section of seed plotting approximate positions of chief sections used in this paper; 18, reconstructed longitudinal section (*c*, canopy; *e*, megagametophyte [endosperm]; *l*, lagenostome; *m*, megaspore membrane; *mi*, micropyle; *n*, tapetal layer of nucellus; *pc*, plinth cavity or pollen chamber; *pl*, plinth; *po*, pollen grains; *sa*, sarcotesta; *sc*, sclerotesta; *vb*, vascular bundle). ×11; 19, cross-section (508a). ×11; 20, semi-diagrammatic drawing of radial section of testa showing sarcotesta and the two zones composing sclerotesta. Note shrunken protoplasm in prismatic cells (514). ×93; 21, tangential section of same. ×93; 22, tangential section of epidermis of plinth (515c). ×93; 23, tangential section of wall of lagenostome showing sculptured cells (506). ×93; 24, diagrammatic representation of summit of seed showing development of pollen chamber and method of pollination. Fig. 25, cross-section of seed of *C. quadratum* (518b), legend as in fig. 18. ×22.

shown in cross-section in figures 19 and 49 has the same relative proportions, its length must be about 4.5 mm. In transverse section the seeds show their platyspermic nature. Preparation 502 (fig. 34) measures 1.5 by 0.9 mm., maximum and minimum diameters, and the other specimen (507c, fig. 19) measures 2.5 by 2.0 mm. In both cases the flattening was in the plane of the seed which includes the two vascular bundles. In the first specimen the sclerotesta is somewhat thickened above the vascular bundles, but the other shows no indication of increased thickness. In no case were there any ridges in the testa such as is characteristic of *C. oblongum* and *C. anglo-germanicum*.

The internal form of the testa is, in the main body of the seed, similar to the exterior. The summit is dome-shaped, however, and passes into the funnel-like lower end of the micropyle. At the apical end of the seed the testa is markedly thickened to form the canopy.

The integument consists of three distinct zones. From the exterior inward they are: the sarcotesta, the sclerotesta, and a delicate thin walled zone through which the vascular bundles progress. The sarcotesta consists of a single layer of light colored cells investing the external surface of the seed. At the apex the cells of this layer are much enlarged to form a fleshy cap to the seed. The length of these cells is 160 μ, which is in contrast to the thickness of about 40 μ for the sarcotesta of the remainder of the seed.

There is some doubt as to the true shape of the apical end of the seed. In two specimens (503–504 and 505–512) the seed appears to be truncated abruptly, the enlarged epidermal cells forming a cylinder surrounding a wide and squarely truncated canopy (figs. 32, 35). In 515c (fig. 33) the canopy appears to be of the more nearly normal dome shape, however, with the sarcotesta reaching to its summit and surrounding the micropyle. The writer is inclined to the view that the truncated appearance of the other specimens is due to destruction of tissue prior to fossilization. He has therefore shown a complete sarcotestal cap in his reconstruction (fig. 18).

As its name implies, the sclerotesta is made up of sclerotic, thick walled elements, its thickness varying from 0.1 to 0.23 mm. in various seeds. There are two distinct layers of tissue making up the sclerotesta (fig. 20). The outer layer consists of a single series of

palisade cells, the inner of elongated sclerotic cells disposed longitudinally. The amount of this tissue is variable; in some cases the palisade layer constitutes most of the integument, in others the longitudinally elongated elements make up one-third of the thickness. The cells of the prismatic layer are roughly hexagonal in cross-section (fig. 21). The cells are extremely thick walled and have a narrow lumen. The shriveled protoplasmic contents (fig. 20) show as black specks, and give to the integument, as seen in section, a peculiar peppered appearance.

A single vascular bundle enters the chalazal end of the seed, and after penetrating to the inner layers of the integument, divides into two. These branches are in the plane of the major diameter of the seed, and lie in the inner layers of the integument, just outside the nucellus. Whether they extend into the canopy could not be determined from the specimens, but by analogy with *Conostoma oblongum* it is probable that they do. As seen in cross-section, the individual bundle consists of about eight or nine tracheids exhibiting scalariform thickenings (fig. 34).

The nucellus falls into three regions: (1) the lagenostome, which arises from the base of a cuplike depression at the summit of (2) the plinth or distal portion of the nucellus, and (3) the main part of the nucellus, now almost completely replaced by the growth of the megagametophyte within it. The nucellus is undiverged from the integument except for the cuplike depression at the summit of the plinth, and for the lagenostome. This differs from the two previously described species in which the nucellus was free from the integument at the level of the plinth.

The body of the nucellus has been almost completely replaced by the growth of the megagametophyte, whose limits are marked by a brown line representing the megaspore membrane. Only in one specimen (section 514) is there any gametophyte tissue preserved, and in this the preservation is extremely poor. All that can be distinguished are a few delicate parenchyma cells. Of the nucellus only the tapetal layer remains, and this is crowded between the megagametophyte and the integument. This tapetal layer consists of extremely large flattened cells of polygonal outline (fig. 36), measuring about 150 μ in diameter by 40 μ in thickness.

LAGENOSTOME AND PLINTH.

These two organs, which form the summit of the nucellus, are so intimately related that they may most conveniently be dealt with together. The distal portion of the plinth is occupied by the plinth cavity (fig. 18 *pc*). The proximal portion of the plinth was occupied by nucellar tissue. With the exception of a plug of crushed tissue at the base of the lagenostome, none of this tissue is preserved, but the boundary between this and the plinth chamber is marked by a faint brown line. Apart from these remains of internal filling tissue, the plinth is represented only by the epidermis which, where its structure is well enough preserved, is seen to consist of a single layer of flattened epidermal cells without special sculpturing (fig. 22).

Following the epidermis of the plinth down the slope of the cup at its summit, it becomes evaginated to form the lagenostome. Thus the epidermis of the plinth and of the lagenostome is one continuous structure. The lagenostome, as in *Conostoma oblongum*, is a tiny goblet-shaped body, the cavity of which communicated with the plinth cavity at the time of pollination. Unlike *Physostoma* and *Lagenostoma*, the mouth is unprovided with any tube or beak. Although none of the specimens studied shows it, by analogy it seems probable that the mouth engaged with the micropylar tube by means of a bevelled flange such as is found in *C. oblongum*. The lagenostome measures 170 μ in maximum diameter by about 150 μ in height (fig. 35). The wall of the lagenostome is formed of a single layer of cells which have an elaborate tracheid-like sculpturing (fig. 23). The floor of the lagenostome does not consist of differentiated sculptured cells but is occupied by a pad of crushed nucellar tissue, the individual cells of which are for the most part indistinguishable. The formation of this pad will be discussed later in connection with the method of pollination. The plinth chamber (fig. 18) lies at the very summit of the nucellus. It is annular in shape and approximately triangular in cross-section. It is bounded on the inside by the epidermis of the depressed cup at the summit of the nucellus; on the outside by the undiverged nucellus and integument; and below by nucellar tissue. This plinth cavity functioned as a pollen chamber, and it is within this cavity that the pollen is nearly always found. In only one case (fig. 3) was any pollen found in the lagenostome.

The pollen grains are multicellular, elliptical in form, and measure 50 by 65 μ in diameter. In common with other Paleozoic seeds there is no evidence of the development of pollen tubes. The absence of pollen tubes and of embryos in Paleozoic seeds may possibly both be due to the same cause, namely, that the "seeds" so far studied are really ovules. The fact that the integument is made up of thick walled stony cells is not incompatible with this view, since in modern gymnosperms, as in the cycads and some conifers, the integument may have become sclerotic before the archegonia are developed.

An outline of the probable course of events in the history of ovular maturation and pollination will help in understanding the relationships of the various parts. At an earlier stage of development than any represented by the preparations, the tip of the nucellus must have been occupied by a soft internal tissue which filled the lagenostome and the plinth, the tissue being continuous from one to the other through the narrow orifice by which these structures communicated (fig. 24 *a*). As the time of pollination drew near, the filling tissue of the lagenostome and the summit of the plinth doubtless underwent degeneration (fig. 24 *b*). A pollination drop was exuded at this time. It was probably formed in part by the mucilaginous substances resulting from disintegration of the internal tissues of the lagenostome and plinth, and in part by secretion from the tracheid-like sculptured cells which make up the walls of the lagenostome. The pollen was caught by this exuded drop, which, as it dried, carried the pollen grains through the lagenostome into the plinth chamber (fig. 24 *c*). The plinth cavity was then closed by the growth of the "tent-pole" of the megagametophyte. This forced the overlying nucellar tissues against the base of the lagenostome, thus sealing the opening (fig. 24 *d*).

Two species have previously been described, *Conostoma oblongum* and *C. anglo-germanicum*. *C. platyspermum* shows more features in common with the former species. In its general proportions and the relation of its height to width, it bears a much stronger resemblance to the former; indeed, in proportion to its length it is even broader than that species. Also, in its platyspermy and in the absence of ridges or wings it resembles *C. oblongum* more closely. In the reduced number of vascular bundles, however, it shows agree-

ment with *C. anglo-germanicum*, and with *Gnetopsis elliptica*, another seed belonging to the *Conostoma* group. In view of the platyspermic nature of *C. oblongum*, *C. platyspermum*, and *Gnetopsis elliptica*, it is interesting to note that in *C. oblongum* there are six vascular bundles, one beneath each of the two major angles of the seed and four intermediate bundles. In *Gnetopsis* the bundles corresponding to the major angles have been lost. In *C. platyspermum*, on the other hand, only the two bundles corresponding to the major angles of the seed are present.

Conostoma quadratum sp. nov. (preparations 517–519)

DIAGNOSIS.—Seed squarish in cross-section. Ribs absent. Radispermic with four vascular bundles. Diameter 1.35 mm.

A number of closely spaced transverse sections of a small seed were obtained by the film method from coal ball C 237. Only the basal portion of the seed is known, as the apical portion was lost in the primary saw cut.

The seed is extremely small, measuring only 1.35 mm. in diameter. The general arrangement of its tissues (figs. 25, 37) is that of a member of the *Conostoma* group. The integument consists of a sarcotesta comprising a single layer of epidermal cells, and a sclerotesta comprising an outer prismatic zone and an inner non-prismatic zone. Four vascular bundles, each corresponding to a corner of the seed, run longitudinally in the now empty space between the integument and nucellus. In the cross-sections the nucellus appears to be free from the integument, owing partly to shrinkage and partly to disintegration of the delicate tissue which formed the innermost part of the integument. The loss of tissue makes it appear as if the nucellus were free from the integument. The same appearance is seen in cross-sections of *C. platyspermum* but in that case the longitudinal sections leave no doubt at the non-divergence of the nucellus and integument. The limits of the megagametophyte are defined by the megaspore membrane. The testa is variable in thickness, measuring 90–180 μ. This variation bears no relation to the vascular strands nor to the symmetry of the seed (figs. 25, 37).

The sarcotesta is relatively more extensive than in the other species of *Conostoma*, as it makes up one-third to one-half the thickness

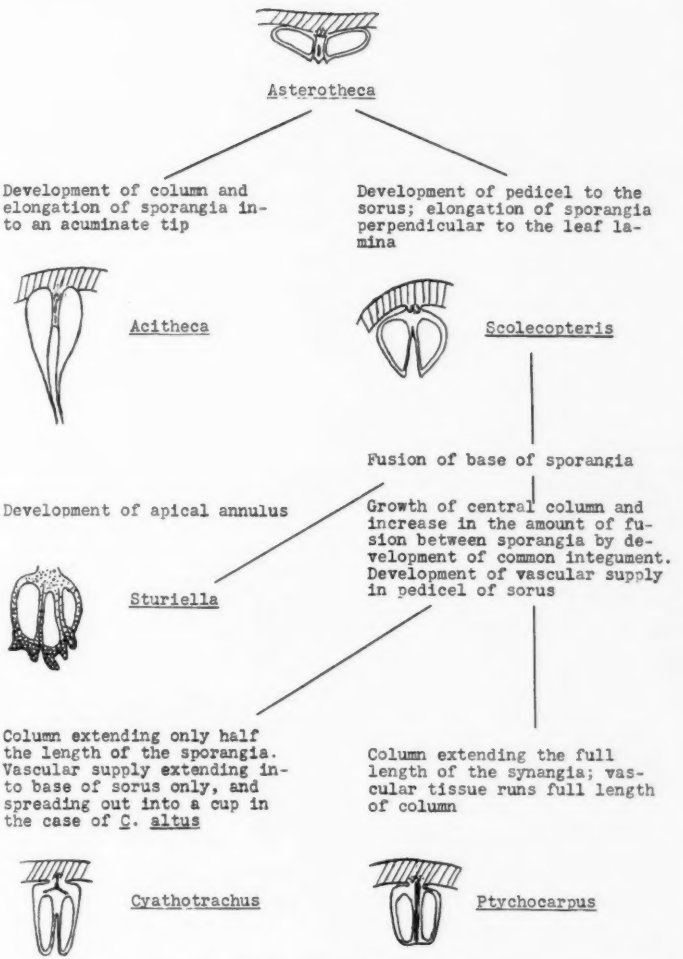

Asterotheca
Development of column and elongation of sporangia into an acuminate tip
Development of pedicel to the sorus; elongation of sporangia perpendicular to the leaf lamina
Acitheca
Scolecopteris
Fusion of base of sporangia
Development of apical annulus
Growth of central column and increase in the amount of fusion between sporangia by development of common integument. Development of vascular supply in pedicel of sorus
Sturiella
Column extending only half the length of the sporangia. Vascular supply extending into base of sorus only, and spreading out into a cup in the case of C. altus
Column extending the full length of the synangia; vascular tissue runs full length of column
Cyathotrachus
Ptychocarpus

FIG. 38.—Provisional family tree showing relations among genera of the Asterothecaceae.

of the testa, and there appears to be no tendency for it to be exfoliated. The sclerotesta consists of two zones, a prismatic zone on the outside and a non-prismatic one on the inside. The prismatic zone is made up of a single layer of stout cells averaging 20 μ in diameter and 40–50 μ in length. The inner zone of the sclerotesta is made up of what appears in transverse section to be isodiametric thick walled cells. By analogy with those of closely related seeds, these cells probably are really longitudinally elongated.

The four vascular bundles are found at the corners of the seed in the empty space lying between the sclerotesta and the nucellus. In some places there are slight traces of a delicate parenchyma which formerly occupied this space. Each vascular bundle consists of about twelve minute tracheids, approximately 3 μ in diameter. The type of tracheal sculpturing could not be resolved very well but it appeared to be scalariform. The sections at the chalaza show that a single vascular bundle enters the seed and passes into the inner layers of the integument, where it divides to give rise to the four bundles.

Only the tapetal layer of the nucellus is preserved. It consists, as in *Conostoma platyspermum*, of the large platelike polygonal cells. The megaspore membrane is for the most part in contact with this layer. Where this is not the case, the condition is probably due to shrinkage. No endosperm is preserved.

The undiverged nucellus, and the fact that the vascular bundles run in the innermost region of the integument, place this seed in the group Lagenostomales. Unfortunately micropylar sections are lacking, so that the most characteristic structures on which the classification of this group is based are absent. However, the structure of the integument is that typical of the Conostomae (**7**). In this group there are but two genera, *Conostoma* and *Gnetopsis*, and the similarity of the latter genus to the former may possibly warrant its inclusion in *Conostoma*. In view of this fact, this seed is assigned there provisionally. The discovery of other specimens showing the micropyle and lagenostome will of course be necessary to confirm this classification. Having regard to the squarish cross-section of the seed, the name *Conostoma quadratum* is proposed.

As far as limited material permits one to say, *C. quadratum* agrees

more closely with *C. anglo-germanicum* than with any other species. In common with that species, the sarcotesta is more extensive and persistent than in the other species. It also agrees in having radial symmetry and four vascular bundles. It differs markedly from that species in the entire absence of ribs, and it is much smaller in size. In the absence of ribs it shows agreement with *C. platyspermum*, from which, however, it differs markedly in other respects, as in general shape of the seed and in the histological structure of the integument (*cf.* figs. 19 and 25).

Summary

1. A morphological study was made of plant material preserved in coal balls from Calhoun coal mine, Richland County, Illinois. The geologic horizon is Middle Conemaugh, early Upper Pennsylvanian.

2. Preparations were made by the cellulose peel method.

3. Seven plants are described in detail. Of these, four are sporangia of ferns, one is the microsporangium of a pteridosperm, and two are seeds. The plants described are: **Notoschizaea robusta** gen. et sp. nov., **Scolecopteris latifolia** sp. nov., *Scolecopteris minor* Hoskins, **Cyathotrachus bulbaceus** sp. nov., **Telangium pygmaeum** sp. nov., **Conostoma platyspermum** sp. nov., and **Conostoma quadratum** sp. nov.

4. A short discussion of the ferns belonging to the Asterotheceae is given, with a phylogenetic tree showing probable relationships.

5. It is suggested that the absence of tubes in the pollen found in the pollen chambers of Paleozoic seeds and the absence of embryos may possibly be due to the same cause, namely, the fact that the so-called seeds are really immature ovules.

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EXPLANATION OF PLATES VIII, IX

PLATE VIII

FIG. 26. *Notoschizaea robusta:* transverse section of sorus (552a). ×50.

FIG. 27. *Scolecopteris latifolia:* cross-section of pinnule (543b). ×37.

FIG. 28. *Cyathotrachus bulbaceus:* transverse section of synangium (540). ×55.

FIG. 29. Longitudinal section of synangium of same (541c). ×55.

FIG. 30. *Telangium pygmaeum:* two synangia in longitudinal section attached to rachis; other synangia cut obliquely (546). ×45.

FIG. 31. *Conostoma platyspermum:* internal cast of seed (*pl*, plinth; *tp*, "tent-pole" or beak of endosperm) (501). ×33.

PLATE IX

Conostoma platyspermum

FIG. 32. Obliquely longitudinal section of seed (503f). ×30.

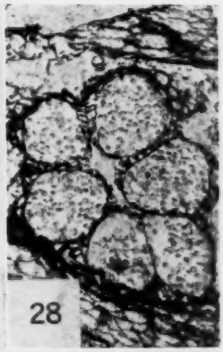
FIG. 33. Same showing complete canopy (515). ×30.

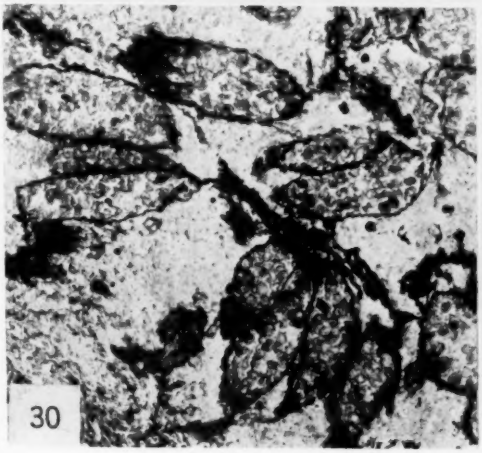
FIG. 34. Transverse section showing vascular bundles (*vb*) (502b). ×33.

FIG. 35. Longitudinal section of apical portion of seed (*i*, integument; *l*, lagenostome; *mi*, micropyle; *mm*, megaspore membrane; *pc*, plinth cavity) (506c). ×60.

Fig. 36. Tangential section showing sclerotesta (*scl*) and tapetal layer of nucellus (*n*) (504h). ×30.

FIG. 37. *Conostoma quadratum:* cross-section of seed. ×50.





GRAHAM on PENNSYLVANIAN FLORA

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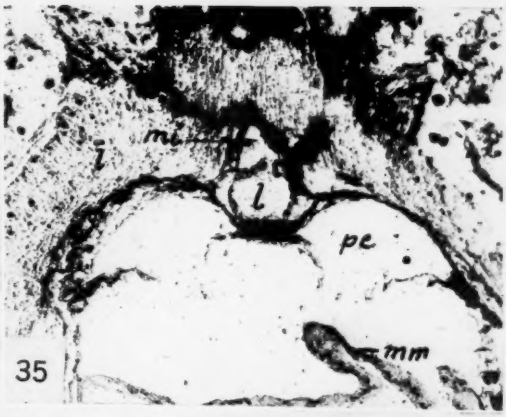
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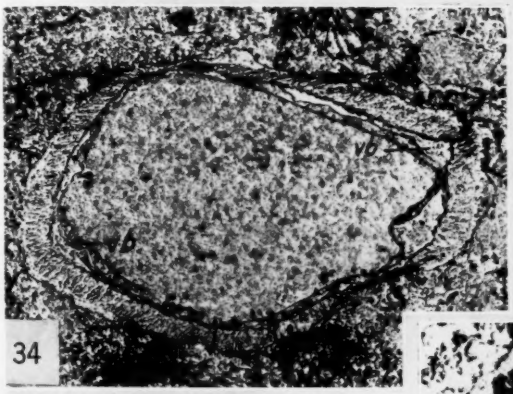
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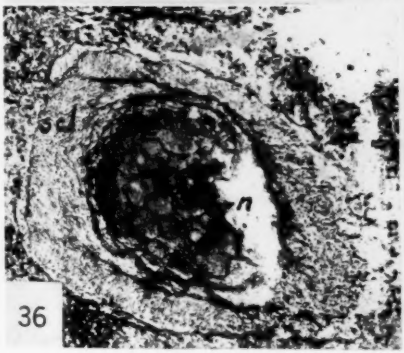
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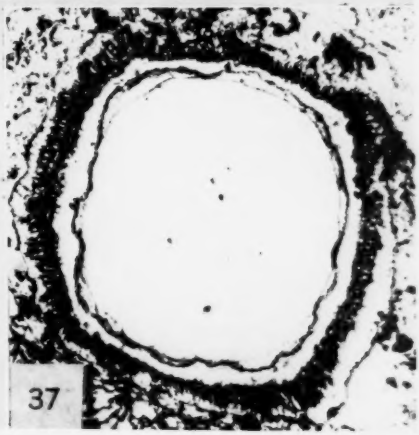
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MALE GAMETOPHYTE OF ATRIPLEX HYMENELYTRA

FREDERICK H. BILLINGS

(WITH ELEVEN FIGURES)

Introduction

Atriplex hymenelytra is a low statured, dioecious shrub which grows in certain parts of the Mojave and Colorado deserts in southern California. Because of its holly-like leaves it is popularly known as desert holly, or silver holly, the latter name having reference to its white leaves. *Atriplex* is represented in California by both monoecious and dioecious species, numbering twenty-nine in all according to JEPSON (4). Ten of these species are reported as dioecious.

The chief purpose in undertaking a study of this species was to ascertain the type of chromosome sex mechanism. The material on which the observations were based was gathered near Barstow on the Mojave desert, in February and March, at which time of year winter rains are generally sufficient to enable shrubs to put forth a new crop of leaves and flowers. Young buds were fixed in Carnoy's fluid, mounted in rows on cardboard squares, imbedded in nitrocellulose and sectioned on a sliding microtome. Iron-alum haematoxylin was used as a stain.

Observations

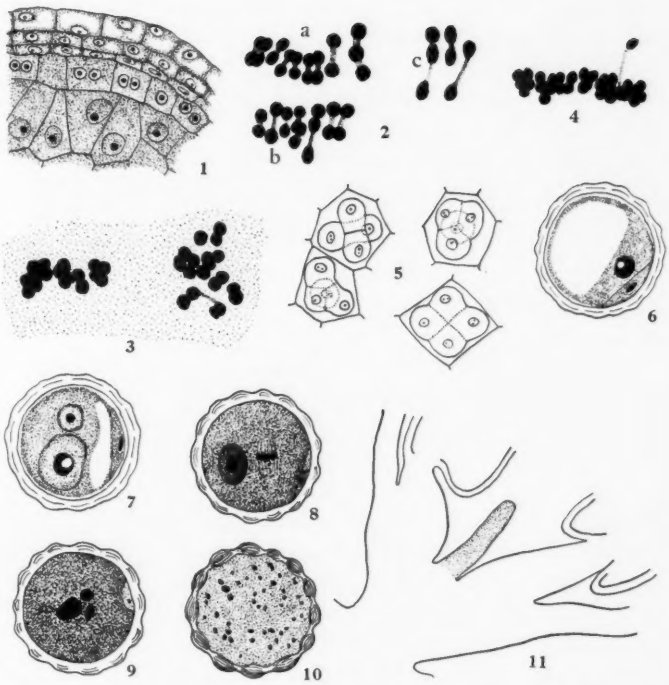
The archesporium arises from hypodermal cells which through periclinal divisions differentiate an inner sporogenous tissue and an outer parietal layer. The maturity of the pollen mother cells is approximately contemporaneous with the completion in development of a tapetum, which is composed mainly of binucleate cells with rich cytoplasmic contents (fig. 1). Meiosis occurs simultaneously in the mother cells of any single anther. The chromosomes that arrange themselves on the metaphase plate are short and slightly elliptical in outline. The process of division is normal, that is, without lagging chromosomes or extruded chromatin. Nine was found to be the haploid number in some of the daughter cells, ten in others, the variation

depending on whether the cell inherited a Y-chromosome along with the eight autosomes, or a bipartite X. Nine appears to be a common N number in the Chenopodiaceae, as may be seen from the following list of species:

SPECIES	N	AUTHORITY
Chenopodium album	9	WINGE
C. hybridum	9	"
C. murale	9	"
C. vulvaria	9	"
C. bonus henricus	18	"
Atriplex hastatum	9	"
A. litorale	9	"
A. patulum	18	"
Beta maritima	9	"
Bassia hirsuta	9	"
Hablitzia tamnoides	9	DAHLGREN
Spinacea oleracea	6	WINGE

In *Atriplex hymenelytra*, one of the chromosomes that appears on the metaphase plate in the heterotypic division is not a continuous structure, but is tripartite (fig. 2*a*). In this particular meiotic figure it stood well away from the remaining eight so that an unobstructed view was obtained. The individual elements were approximately equidistant from one another, with no indication as to which one would separate from the other two. The elements were globose in form and about equal in size, the entire tripartite structure measuring 3.1 micromillimeters in length. To all appearances there were three separate and distinct chromosomes, all of about the same size and form as the other chromosomes. In anaphase, a terminal one separates from the other two, which then draw closer together. The best views of this stage were obtainable when a portion of the chromosome group was cut away (fig. 2 *b*, *c*). The next stage observed was one in which a double member was seen at one of the poles (fig. 3). Counting the bipartite member here seen as two separate chromosomes, the number was found to be ten. It is apparent that there is a partial fusion of the elements after they have reached the poles.

A homoeotypic division is represented in figure 3, in which a polar view of one metaphase plate is obtained and a side view of the other.



FIGS. 1–11.—Fig. 1, pollen mother cells and binucleate tapetum just before meiosis. ×400. Fig. 2, heterotypic metaphase (*a*, 8 autosome bivalents and a tripartite X–Y group with elements equidistant from one another; *b*, *c*, incomplete chromosome groups, but ones in which disjunction of Y from a bipartite X is clearly indicated). ×2700. Fig. 3, homoeotypic metaphase. One chromosome group shows separation of the daughter bipartite X's with an N count of 10; the other group, probably containing the Y, gives an N count of 9. ×2700. Fig. 4, somatic metaphase taken from cell in anther wall; 18 chromosomes. ×2700. Fig. 5, diagrams illustrating various groupings of microspore tetrads. Fig. 6, vacuolated 2-celled male gametophyte with one cell walled off, and resembling a prothallial cell. ×700. Fig. 7, 3-celled male gametophyte. Tube and generative nuclei free in main cavity. ×700. Fig. 8, 3-celled gametophyte showing division of generative nucleus. Nucleus of walled-off cell undergoing disintegration. ×700. Fig. 9, mature 4-celled gametophyte. ×700. Fig. 10, mature pollen grain showing complete nuclear disintegration. ×700. Fig. 11, diagram of base of a staminate flower at time of anthesis. Gynoecium reduced to a sterile column of tissue. ×42.

Examination of the chromosomes shows that there is a double member on one plate but not on the other. Separation of the bipartite daughter chromosomes has proceeded in advance of the others.

A somatic division obtained from one of the cells in an anther wall is represented in figure 4. No bipartite chromosome was observed here, so it was inferred that it is an element in the chromosome complement of the pistillate plant. Precocious separation of a single pair is shown.

In both plants and animals in which a tripartite chromosome appears in the heterotypic division, the structure has been interpreted by certain investigators as consisting of three chromosomes, in which case an extra chromosome is allotted the daughter nucleus receiving the bipartite X. For example, MEURMAN (6) found in *Rumex acetosella* an X-Y type which resembles that found in *A. hymenelytra*, in that it is tripartite. Apparently it differs, however, in that the X is constricted only and is not divisible into two separate elements in an earlier state. The middle segment in *R. acetosella* is considerably the largest of the three. In anaphase the Y disjoins from the constricted X. In polar view of the homoeotypic metaphase plate, the X member can be seen as bipartite. In *A. hymenelytra* the three elements of the tripartite X-Y complex are approximately the same size. It would seem to be a matter of minor importance whether the elements are of equal size or not. In *R. acetosella* the daughter nucleus receiving the constricted X is reported as having a total count of twenty-one (nineteen autosomes and the X which is counted as two); whereas the other daughter nucleus, carrying nineteen autosomes and the Y, is credited with twenty. In *R. acetosa*, the tripartite structure as seen by KIHARA and ONO (5) varies in its behavior from *R. acetosella* and *A. hymenelytra*, in that both terminal segments pass to the same pole at disjunction, leaving the large middle segment to pass to the other pole. In this instance there is a complete separation of all three portions of the original tripartite chromosome complex, the nucleus receiving the end segments having a count of one more than that receiving the middle member. WILSON (10) regards the two small chromosomes as elements in a Y complex. *R. acetosa* resembles *A. hymenelytra* in possessing three separate and distinct elements as the heterochromosome group.

Interestingly enough, an X-Y system closely resembling that in *A. hymenelytra* is found in the opossum (*Didelphys virginiana*), as reported by PAINTER (7). The X chromosome in this animal is composed of a pair of similar egg-shaped elements which appear together, not only in the maturation divisions but also in the somatic divisions in the female. PAINTER, however, regards the X member as a single chromosome and consequently assigns an equal chromosome count to each daughter nucleus, that is, eleven in the maturation divisions and twenty-two in the somatic divisions of both males and females. WILSON gives a list of insects in which the X is a double member which he regards as two chromosomes, thus giving one half the sperm nuclei an excess of one in the chromosome count. In a species in which the X (or Y) is seen at some time to consist of two separate and distinct elements, there are good reasons for considering such a member as two, even though the elements are in conjunction or partial fusion at another time. On the other hand, one might be tempted to regard a merely constricted chromosome as single were it not for the presence of intergrading or borderline instances in which the constriction becomes so deep or so long as virtually to differentiate two chromosomes. This appears to be the case in the opossum, as shown by some of PAINTER's representations of the X. In *A. hymenelytra*, however, the situation seems fairly clear, inasmuch as three separate and distinct elements, one the Y, appear in metaphase, the X element soon partially fusing to form a constricted chromosome. The N chromosome count for this species may therefore be said to be nine and ten.

Microspore tetrads show some variation in spore arrangement. Generally and typically they are tetrahedral, but other types of groupings are sometimes found, especially that often seen in monocotyledons in which the four microspores are located in the same plane (fig. 5).

On separating, the mature microspores enlarge and undergo a vacuolation, the nucleus taking a position near the wall. Here a division occurs that forms a 2-celled male gametophyte. In some instances at least, one of the daughter nuclei takes a position close to the microspore wall, where it may become separated from the sister nucleus and the main portion of the microspore contents by a wall

(fig. 6). It is not always possible, however, to observe the wall; but whether it is organized as a cell or not, the nucleus generally remains more or less fixed in position and fails to undergo further division. The nucleus in the main cavity of the microspore now divides to form the generative and tube nuclei (fig. 7). Figures 6 and 7 are stages in the development of a microspore in which a definite cell is cut off to take a position next to the wall, as just described. The division of the generative nucleus to form the sperm nuclei is shown in figure 8, while in figure 9 a mature 4-celled pollen grain is represented. In these last two stages the vacuoles seen in earlier stages have disappeared. The cytoplasm in the mature grain is rather dense and the non-functional cell by the wall is in a state of dissolution. Many mature pollen grains show but three nuclei, failure to exhibit the presence of the fourth being due to one of three causes: it may not have been formed in the first place; it may have undergone complete disintegration; or it may not have been lying in the optical section, and hence have escaped discovery. It is not known therefore in what percentage of microspores a 4-celled gametophyte arises.

To all appearances one of the daughter cells of the first division of the microspore nucleus is prothallial in nature, recalling in time of appearance and general position the first of the two prothallial cells developed in the male gametophyte history of some of the gymnosperms. Instances that occur among angiosperms, however, have been reported by CHAMBERLAIN (2) in *Lilium tigrinum;* by SMITH (9) in *Eichornia crassipes;* by CAMPBELL (1) in *Sparganium simplex;* and by WÒYCICKI (11) in *Yucca recurva.* COULTER and CHAMBERLAIN (3) regard the appearance of the fourth nucleus as sufficiently rare to cause them to hesitate in assigning to it a definite prothallial morphology. SCHNARF (8) thinks that all types of instances of excess nuclei in the male gametophyte of angiosperms may be due to such influences as light, temperature, or moisture, but particularly as the result of hybridization. Hybridization is often indicated by irregularities in meiosis and in pollen development, such as lagging chromosomes, extrusion of chromatin, polyspory, defective pollen, etc. The production of defective pollen is well marked in *A. hymenelytra.* Grains may undergo degeneration, in which instance the cytoplasm is generally intact, but fragmentation of the nuclei takes place

(fig. 10). In other instances, anthers can be found with normal pollen intermixed with empty or undersized grains, the defective portion amounting to as much as 32 per cent. In still other instances entire anthers abort and develop no normal pollen. Thus it is possible that hybridization has occurred at some time, and if so, it might be a factor in accounting for the irregularity of excess number in the male gametophyte, and also for the production of so much defective pollen. With respect to the fourth nucleus or problematical prothallial cell on the other hand, it should not be considered so remotely improbable that an angiosperm would now and then be found exhibiting an atavistic tendency sufficient to conserve an ancestral vestige such as a prothallial cell in the male gametophyte.

At the time of anthesis, the gynoecium in the staminate flower is seen to be reduced to a slender column of tissue showing no differentiation that would in any way indicate its probable morphology (fig. 11).

The embryo sac in *A. hymenelytra* is an 8-celled gametophyte.

Summary

1. The development of the pollen mother cells from the archesporium follows the usual course found in angiosperms.

2. The tapetum is composed of binucleate, richly protoplasmic cells.

3. Meiosis appears to be normal.

4. Eight autosome bivalents and a tripartite X-Y group appear on the metaphase plate in I. The X element is composed of two separate chromosomes. The N count is nine and ten.

5. Microspore tetrads show variation in grouping, the predominant type being tetrahedral.

6. Certain microspores undergo three nuclear divisions, one of the first two nuclei formed organizing as a cell that strongly resembles a prothallial cell.

7. A considerable number of pollen grains show abnormalities such as disintegrating nuclei, under size, or absence of cell contents.

8. The gynoecium in staminate flowers is reduced to a column of undifferentiated tissue.

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MARINE PLANKTON DIATOMS OF LOWER CALIFORNIA IN 1931

W. E. ALLEN

(WITH ONE FIGURE)

Introduction

At the invitation of the Commander of one of the Mexican Government patrol boats, operating in the waters off Lower California, the Scripps Institution of Oceanography assigned to Mr. P. S. BARNHART, Curator of its museum, the task of making a series of observations on fisheries conditions and occurrence of phytoplankton (ocean pasturage) in the spring of 1931. In the course of this cruise Mr. BARNHART was able to make 140 collections of surface material at numerous points along or near the west coast of Lower California and at a few points in the Gulf of California (fig. 1). All of these collections were made merely by dipping up from the surface a certain quantity of water (three gallons in this series) and filtering through a small conical net of no. 25 mill silk, with meshes averaging about 0.05 mm. in diameter.

The first catches were made on April 11, 1931, and the last on May 2, 1931, the whole series being taken in a period of about three weeks. Mr. BARNHART had made a similar cruise in 1922, on which he accumulated a series of collections of similar character and extent, but that cruise was made in July (**2**). A shorter series of catches obtained by the California Academy of Sciences along the west coast of Lower California in 1921 was taken in April, although a little earlier (**1**). While these differences in time, localities, and numbers of catches in the three series may not appear significant, it is evident from experience with occurrence of plankton organisms that they are great enough to prevent any possibility of exact comparisons. However, there is considerable information to be obtained from general comparisons.

The numbers of dinoflagellates were negligible throughout all of the catches of this series. For that reason they will receive no partic-

SAN DIEGO
PT. BANDA
C. COLNETT
C. SAN QUENTIN
MEXICO
30°
SACRAMENTO RF.
GUADALUPE ISL.
CERROS ISL.
PT. SAN EUGENIO
LOWER
CALIFORNIA
PT. SAN PABLO
GULF
OF
CALIFORNIA
PT. ABREOJOS
PT. SAN JUANICO
25°
C. SAN LAZARO
LA PAZ
PALMAS BAY
MAP OF
LOWER CALIFORNIA
115°
C. SAN LUCAS
110°

FIG. 1

ular attention. Diatoms were the only other constituents of the phytoplankton which appeared in notable numbers at any time. On that account, the remainder of this report will deal with these organisms. Records of good and bad condition, as well as of numbers present, were made for each catch.

Differences in abundance of diatoms in collections made in different localities represented in this series occurred in such a way as to make it convenient for discussion to designate four regions in the territory covered (fig. 1), only one of which gave notable evidence of productivity: (1) northern region, comprising the territory north of Pt. San Eugenio; (2) middle region, comprising the territory from Pt. San Eugenio to and including Magdalena Bay; (3) southern region, from Magdalena Bay environs to Socorro Island (not shown on this map) about 260 miles south of Cape San Lucas; (4) Gulf region, comprising the localities in the Gulf between La Paz and Cape San Lucas.

Observations

1. Northern region

On the south-bound part of the trip on April 14, 21 catches were made between San Diego and Guadalupe Island. These were taken rather near shore to Cape Banda, getting farther and farther to seaward after passing that point until about 150 miles off-shore at the island. The abundance was very low in all of these catches, although several showed the presence of a number of different species, the largest showing being nine species about 40 miles seaward from Cape Colnett. None of the five catches between Guadalupe Island and Pt. San Eugenio was as prominent as this. On the return trip a catch near Cerros Island on April 30 showed ten species, another near Sacramento Reef on May 2 showed eleven species, and another near Cape Colnett on May 2 showed thirteen species. For the region in general, such records indicate the possibility of considerable or high abundance occurring at other times, at other points not sampled, or at levels beneath the surface. It is not probable that a desert region would show this diversity of species, many representatives of which were in good condition. As a matter of fact, the Barnhart series of 1922 gave direct evidence that the indication is stronger than that of mere possibility. In that July series 23 catches out of

88 yielded numbers of diatoms greater than 10,000 cells to the liter; and in the Pt. San Quentin section 14 catches out of 39 yielded more than 10,000 and one was greater than 100,000 cells per liter, many of the smaller catches being off-shore toward Guadalupe Island.

2. Middle region

In 1931 the middle region was distinct from the others by reason of the great abundance of diatoms shown in 19 out of the 29 catches made while running southward. In fact, 13 of these catches were of the order of magnitude of millions of cells per liter, an abundance great enough to be notable in any region yet investigated by the Scripps Institution from the coast of Peru to the Aleutian Islands. For a period of three hours, approaching Pt. Abreojos on April 16, the boat ran through water of a rusty tinge ("red water" to some observers) in which the abundance of diatoms was great enough to cause the discoloration. The largest single catch in the region (3,933,921 cells per liter) was made a little farther north near Thurloe Head (southeast of Pt. San Eugenio) at 7:15 A.M. on the same day. On the return trip on April 30 a catch yielding more than 1,000,000 cells per liter was taken in Magdalena Bay near Man o' War Cove and a fairly large catch near Cape San Lazaro, but catches following these were small, possibly in part because of being taken a little farther off-shore. In the series of 1921 and of 1922, the part of this region near Pt. Abreojos yielded the largest catches as well as the greatest number of larger catches, but in both series the largest catches were small or insignificant compared with the large catches of 1931. Still the showing of maximum abundance in the region in different years and seasons is an important indication of a tendency to good productivity in it as compared with others. Water temperatures with catches reaching more than 1,000,000 cells per liter ranged from 16.3° to 18° C.

3. Southern region

Up to and including 1931, no series of collections of phytoplankton has been obtained which showed catches of any significance from the open ocean between the general locality of Magdalena Bay and the Revillagigedo Islands nearly 300 miles to the south. In 1931 the

several catches taken in the region showed the presence of a few diatoms in every case, and it seems possible that notable abundance may occur at times not yet noticed, or that there may be notable abundance at depths below the surface which have not been sampled. It seems fair, however, to say that good productivity of plankton diatoms is not to be expected in the region.

4. Gulf region

The 1921 series is the only one which comprised collections from the Gulf of California prior to 1931. The evidence from the catches of both years agrees in showing only very small catches in the lower part of the Gulf, all being near the shores of the peninsula on the west side of the Gulf. Nine species of diatoms and seven species of dinoflagellates were represented in one of the catches of 1931, however, and it may be supposed that there are times in some years when a considerable abundance might be found.

Forms represented

In study of the material, genera of diatoms to the number of 29 were recorded, and species to the number of 46. It is probable that a number of species were overlooked, or not recognized under the low magnification used in enumeration, and a few genera may have been overlooked also; but if so their numbers must have been too small to be significant in a study mainly concerned with problems of productivity or occurrence of abundance.

Six genera, *Bacteriastrum*, *Chaetoceros*, *Coscinodiscus*, *Nitzschia*, *Rhizosolenia*, and *Thalassiothrix*, were represented in all four regions. It is probable that these genera are the six most regularly represented in the thousands of collections made by the Institution in California waters in the last 16 years. Their wide spread in the catches of this series indicates a tendency for the Lower California territory to support populations of pelagic plants generally similar in character to those somewhat farther north. In a few of the large catches of the middle region, two other genera, *Asterionella* and *Skeletonema*, contributed largely to the abundance. These two genera occasionally take the lead in abundance along the California coast, and even farther north.

Four genera and six species were especially prominent in the large catches of the middle region. Of these, *Skeletonema costatum* Grev. was most prominent in more catches than any other single species, although the catchall group, *Chaetoceros* sp., consisting of specimens too small or too poorly marked to be identified, had about equal prominence. *Chaetoceros costatus* Pav. appeared to reach the maximum numbers for a single species in a single catch (about 2,000,000 cells per liter 22 miles south of Pt. Abreojos), but its characters were often so poorly marked that the record is somewhat doubtful. *Chaetoceros socialis* Lauder presented similar aspects and difficulties, the latter increased so far as identification is concerned by its wide range of differences in the size and form of cells and in the extent of their attachment in colonies. *Nitzschia seriata* Cl. showed greatest prominence amongst the components of only one catch (11 miles south of Pt. Abreojos), and *Asterionella japonica* Cl. was first only in the catch from inside Magdalena Bay. Thirty-eight of the other species listed more or less frequently, and in larger or smaller numbers in the catches of this series, are commonly found in series of collections made in California waters and northward. Only one species, *Guinardia flaccida* (Castr.), is so rarely found in more northerly catches as to make its presence notable in Lower California. It was not abundant in any catch of this series.

Vitality of specimens

As in examinations of other series of phytoplankton in recent years, an effort was made to estimate roughly the biological condition of populations by keeping a count of those in good and those in poor or decadent condition. South-bound in region 1 nearly all specimens in the small catches were disintegrating or obviously dead. North-bound, a number of catches consisted almost entirely of specimens appearing to be in vigorous condition, judging mainly by the normal form and position of the chromoplasts. In regions 3 and 4 very few normal appearing specimens were found, except for four catches near the lower end of the Gulf of California in which most specimens were in good condition.

In the large catches of region 2 some showed nearly all in poor condition, others nearly all in good condition, but most were char-

acterized by the appearance of certain prominent species being mostly in good condition while others in the same catch were mostly in poor condition. However, *Chaetoceros socialis* was mostly in poor condition in the catches where it was prominent, while *Nitzschia seriata* was mostly in good condition where it was found in abundance. A few species of *Chaetoceros* were also mostly in good condition. These differences in showing in the same catches have two points of interest: (1) The presence of dead or decadent specimens in the surface level in such large numbers makes it difficult to explain the processes involved in flotation or deposit of such microscopic particles in nature. (2) The concurrent occurrence of abundance of species so unlike in their momentary showing of vitality is puzzling, even if it be supposed that one is replacing the other, either through superior vigor or through closer fitness. Considering the opportunity for disappearance of dead frustules by sinking, it might be expected that they would be few where vigorous development of associated forms was occurring.

Subtropical productivity

From time to time one sees some statement or account of marvelous productivity of plankton in frigid seas, sometimes coupled with a comparison with tropic seas in which negligible productivity is stated or implied. Trustworthy data covering the problem of such relative productivity in frigid and tropic seas are not in existence. For that reason, records of abundant occurrence of plankton in tropic or subtropic waters have considerable importance. In this series, catches exceeding a million cells per liter were found over a sailing distance of more than 100 miles near the border line of the tropic zone. These were all taken from the surface level which, on account of more direct sunlight, may not be the most favorable level for photosynthetic organisms, although it may be the most favorable in frigid waters where the radiation is more oblique. Even in frigid areas, it is known that the open sea, and many in-shore localities as well, show scant production at times when abundant production occurs in neighboring localities (3). Furthermore, it seems probable that marine plankton plants resemble land plants in having a longer vegetative period in the tropics than they have in frigid areas. All

things considered, it seems fair to say that while the arctic and antarctic zones cannot be proved to be most productive of marine phytoplankton by existent evidence, neither can the tropics, although such abundance at the surface level as appeared in this series gives reason for suspecting that total productivity, including all levels above 100 meters and all seasons, may be greater in the tropics or in the subtropics.

Summary

1. Great abundance of plankton diatoms was found in surface catches along the coast of Lower California from a locality near Pt. San Eugenio to a locality near Pt. San Lazaro, a distance of more than 100 miles.

2. Greatest productivity appeared near shore (relative to the open sea) and in the general neighborhood of Pt. Abreojos, the locality appearing to be most productive from the evidence of other series.

3. The diatom populations were essentially similar to those of the California coast in respect to component genera and species.

4. Certain of the larger catches contained at least as many dead or decadent specimens as there were of those in good condition.

5. The adaptability and dependability of the measured water method of collecting is well illustrated by the results of this series.

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ANOMALOUS EMBRYOS OF CULTIVATED VARIETIES OF PRUNUS WITH PARTICULAR REFERENCE TO FRUIT BREEDING[1]

H. B. TUKEY

(WITH TWENTY-TWO FIGURES)

Anomalous embryos are not infrequent among plants. Their occurrence in the species type of the sweet cherry (*Prunus avium* L.) and of the peach (*P. persica* Stokes), therefore, would be in itself of no more than passing interest. Their occurrence among cultivated clons or varieties of sweet cherry and peach, however, and particularly their frequency and character, take on added importance because of their relation to systematic fruit breeding. In addition, facts bearing on this situation are important in the commercial production of seedling understocks upon which cultivated varieties of cherry and peach are propagated. Accordingly it has seemed worth while to place on record the observations of anomalous peach and cherry embryos, made as incidental to the removal of embryos from twenty-seven varieties of peaches and seventeen varieties of sweet cherry during a study of peach and cherry development and during the artificial culturing of peach and cherry embryos (**1**, **2**).

Some of the embryos were sectioned from material in paraffin, but most of them were studied as fresh material under the dissecting microscope. The peach varieties used were Alexander Crosby, Arp, Belle of Georgia, Canada, Carman, Champion, Chili, Delicious, Eagle Beak, Early Crawford, Early Victor, Elberta, Foster, Golden Jubilee, Greensboro, Lola, Maule Early, May Lee, Mikado, Morellone, Mountain Rose, Rochester, St. John, Schumaker, Triumph, Troth, Vainqueur, Valiant, Veteran, and Waddell. The cherry varieties used were Abundance, Black Republican, Black Tartarian, Burbank, Coe, Downer, Eagle, Early Purple, Elton, Governor Wood, Knight, Lambert, Mazzard, Napoleon, Oswego, Schmidt, and Windsor.

[1] Approved by the Director of the New York State Agricultural Experiment Station for publication as Journal Paper no. 17.

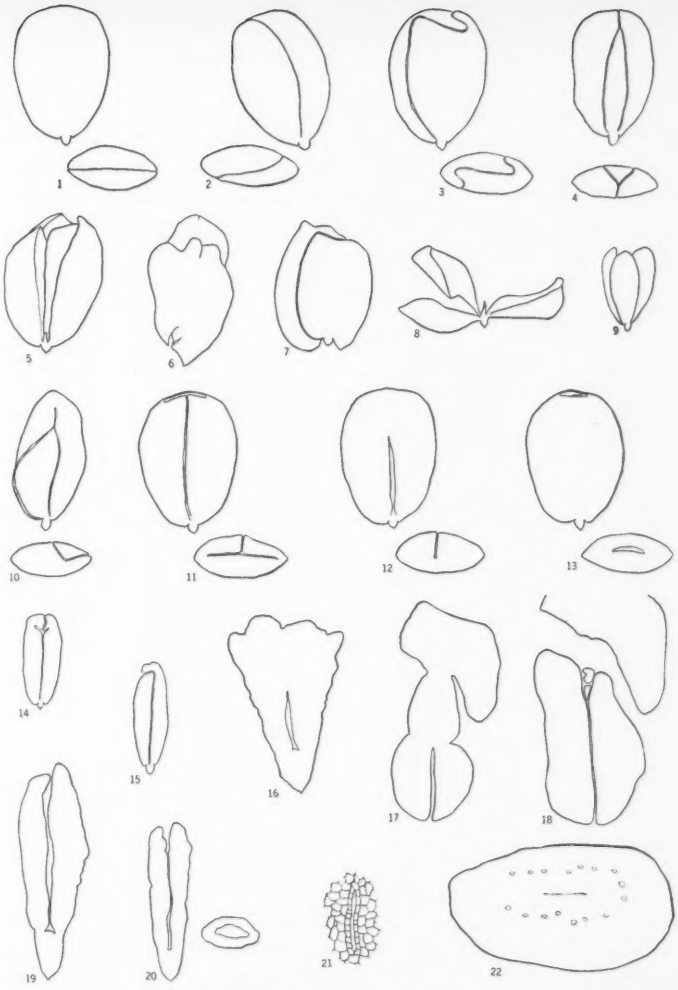
Normal development

The "normal" embryos in the peach and the cherry are similar, with two erect cotyledons of equal size as shown in figure 1. The seed is anatropous, so that the embryo is erect, with the hypocotyl adjacent to the micropyle and the distal end of the cotyledons adjacent to the chalaza.

Anomalous development

Supernumerary cotyledons.—The occurrence of embryos with more than two cotyledons has been found in five varieties of sweet cherry, Early Purple, Burbank, Lyons, Coe, and Downer, and four varieties of peach, Carman, Foster, Elberta, and Chili, from the seventeen varieties of sweet cherry and twenty-seven varieties of peach examined. The frequency is not high, however, so that the possibility is not eliminated that the examination of a greater number of embryos of the other varieties may reveal embryos with more than two cotyledons. All but one of the embryos with supernumerary cotyledons had three cotyledons (figs. 4, 7, 8). One had four cotyledons (fig. 5). Such embryos may germinate (figs. 8, 9) and some have been grown to the development of a seedling 6 inches high by artificial culture on nutrient agar (**2**).

Suppression of cotyledons.—The suppression of one cotyledon in whole or in part is also of frequent occurrence, although more common in the sweet cherry than in the peach. Suppression is of varying degrees. It may occur as the fuller development of one cotyledon than the other (fig. 10). It may occur as the complete suppression of one cotyledon, in which case the developing cotyledon is suggestive of the enfolding single cotyledon (scutellum) of corn (*Zea mays*), a monocotyledon (fig. 11). In other instances the cotyledons may arise undiverged to give the appearance of a closed collar (figs. 13, 16, 19, 20, 22). When the cotyledons are undiverged, the general appearance is as of a single plump cotyledon. Closer examination, however, shows a separation extending as a hollow cylinder from the tip of the cotyledons to the cotyledonary plate. Figure 21 shows in cross-section in detail the close proximity of the inner surfaces and the smallness of the opening.



FIGS. 1–22.—Fig. 1, "normal" peach embryo with two erect cotyledons. Fig. 2, cotyledons facing each other at an angle from the normal. Fig. 3, S-shaped cotyledons. Fig. 4, three cotyledons. Fig. 5, four cotyledons opened to show arrangement. Figs. 6, 7, grotesque shapes. Figs. 8, 9, germinating embryo with three functional cotyledons. Fig. 10, partial suppression of one cotyledon. Fig. 11, entire suppression of one cotyledon (note scutellum-like appearance, as of a monocotyledon). Fig. 12, entire suppression of one cotyledon. Fig. 13, lack of divergence, producing a closed collar-like structure. Fig. 14, cotyledons folded back upon themselves. Fig. 15, one cotyledon folded over the other at distal end. Fig. 16, undiverged cotyledons and proliferation of distal end. Fig. 17, cross-section of 3-cotyledon embryo at cotyledonary plate. Fig. 18, cross-section of 3-cotyledon embryo just above cotyledonary plate. Figs. 19, 20, undiverged cotyledons showing central opening from distal end to cotyledonary plate. Fig. 21, detail of central opening. Fig. 22, cross-section of cherry embryo with undiverged cotyledons showing vascular bundles and central opening.

ANOMALOUS SHAPES.—It is not uncommon to find the tip of one cotyledon folded over the tip of the other (fig. 15), or to find the tips of both cotyledons folded back upon themselves (fig. 14). Still more frequently the inner surfaces of the cotyledons are not flat. Instead the vertical edges of one may practically enfold the edges of the other on one side, and the reverse on the other side, to give a vertical s-shaped appearance (fig. 3). Again, both cotyledons may be turned through nearly 90° so that they face each other at almost right angles to the normal (fig. 2). Other shapes also appear which are often grotesque, as in figures 6 and 7, and occasionally an embryo may develop several true leaves while still inclosed within the integuments.

FREQUENCY OF ANOMALOUS EMBRYOS

Anomalous embryos occur more frequently in some varieties than in others, and more frequently among horticultural varieties than among the wild species types. The Krummel peach for example may show as high as 70 per cent partially developed embryos; Eagle Beak may show as high as 20 per cent malformed embryos; and Foster may show a high proportion of abnormal embryos. On the other hand, Chili seldom shows poorly developed embryos, but frequently produces embryos with three cotyledons. The Downer cherry and representatives of the species type of *Prunus avium* (Mazzard) seldom produce abnormal embryos; likewise so-called "natural" white-fleshed peaches growing in the wild seldom produce anomalous embryos.

These observations serve to emphasize the heterozygous condition in cultivated varieties of peach and cherry, in contrast to the more homozygous condition among the wild species types. The preference of nurserymen for seed in general from wild types rather than from horticultural varieties is shown to have some basis in fact. Plant breeders might find it profitable to begin their study of segregation by an examination of the seed and the embryos from crosses. The factors of anomalous and abortive embryos are more likely to have been overlooked in *Prunus* than in other deciduous fruits, because the seeds of *Prunus* are inclosed in a stony pericarp or pit and

may therefore frequently go unobserved until the seed has either germinated or disintegrated.

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A STUDY IN THE GENUS TETRAMOLOPIUM NEES (FAMILY: COMPOSITAE)

EARL EDWARD SHERFF

Tetramolopium bennettii sp. nov.—Frutex gracilis ramosus 5–8 dm. altus, caule ramisque inferne nudis. Folia secundum ramulos ultimos subconferte disposita, plerumque suberecta, filiformia, crassa, glabrata, supra canaliculata, apice acutiuscula, 1.5–2.5 cm. longa et circ. 0.3–0.4 mm. lata. Capitula tenuiter pedunculata pedunculis minutissime glandulosis 1–3-bracteatis ramulos terminantibus tantum 1–2.5 cm. longis, circ. 1 cm. lata. Involucrum circ. 4 mm. altum, bracteis lanceolato-linearibus acerrimis plus minusve glandulosis et subciliatis. Flores ligulati 30–45, corollis circ. 3.5–4 mm. longis, limbo quam tubo vix vel non breviore. Flores tubulosi ∓16, corollis circ. 3.5 mm. longis culmine purpurascentibus pappum superantibus. Achaenia plana, oblanceolata, brunneo-straminea, adpresse erecto-hispidula, faciebus unicostata vel costa raro geminata, 2 mm. longa.

Specimens examined: *Frederick Debell Bennett* 18, Isl. Maui, Hawaiian Isls., 1833–1836 (type, Herb. Berl.); *Charles N. Forbes*, ridge east of Wainee, Isl. Maui, August, 1910 (Herb. Bishop Mus.); *idem*, Lahainaluna, Isl. Maui, August, 1910 (Herb. Bishop Mus.).

Distinguished from *T. remyi* A. Gray, which it resembles in foliage, by the smaller and more numerous heads, the much shorter peduncles, the many fewer ray florets, etc.

Tetramolopium filiforme sp. nov.—Fruticosa, humilis, ramosa, ramulis foliorum delapsorum vestigiis tectis aliter glabris. Folia numerosissima, filiformia, sparsim setosa, crassa, supra plus minusve canaliculata, apice rotundato-cartilaginea glaberrimaque, tantum circ. 1–1.5 cm. longa et 0.2–0.5 mm. lata. Capitula solitaria ultra folia breviter exserta pedunculis tenuissimis hispidulis 2–3 cm. longis, circ. 1 cm. lata. Involucrum campanulato-hemisphaericum, bracteis 2- vel sub-3-serialibus, anguste vel moderate linearibus, nitidis, apice acutis, tergo glabris vel glabratis, margine minutissime

ciliatis, intimis circ. 3 mm. longis extimis fere dimidio brevioribus. Flores ligulati circ. 30–40, lineares, reflexi. Flores tubulosi ∓12, purpurascentes, tubo limbo multo longiore. Achaenia nitida, brunnea, plana, oblanceolata, marginibus incrassatis glaberrima, faciebus longitudinaliter nunc valde nunc aegre 1-costata et superne sparso-hispida, corpore circ. 2.2 mm. longa, disco epigyno parvo instructa; pappi setis albidis tenuissimis, minutissime antrorso-hispidulis, corpori aequalibus.

Specimens examined: *Dr. William Hillebrand*, Waianae Mts., Isl. Oahu, Hawaiian Isls., 1869 (type, Herb. Gray: cotypes, Herb. Berl.; Herb. Kew).

Tetramolopium polyphyllum sp. nov.—Fruticosa, forsitan humilis decumbensque, ramulis tenuibus inferne foliorum delapsorum vestigiis tectis aliter glabris. Folia caulis apicem versus confertissima (∓25 per 1 cm. caulis), demissa vel summa erecta, tenero-membranacea, angustissime linearia, apice acuta, inferne in petiolos nematoideos 1–1.5 cm. longos elongato-angustata, petiolo adjecto 2–4 cm. longa et 0.4–2.5 mm. lata, 1-nervia nervo supra impresso infra elevato, plana vel plus minusve revoluta, marginibus et nervo mediano hispido-ciliata alibi scabrido-hispidula vel mox glabrata, integerrima vel supra medium minute plus minusve serrulata serraturis in cilia brevia rigida curvato-erecta saepe desinentibus vel raro acerrime 1- vel 2-dentata dentibus inflexis usque ad 2.5 mm. longis. Capitula solitaria, exserta, tenuissime pedunculata pedunculis hispidis 1.5–3 cm. longis bracteatis bracteis filiformibus usque ad 1 cm. longis, circ. 9 mm. lata. Involucrum hemisphaericum vel late obconicum bracteis sub-3-seriatis linearibus acutis minute plus minusve hispidulis ciliatisque, interioribus marginaliter scariosis, extimis ∓1.5 mm. aliis usque ad 3.5 mm. longis. Flores ligulati ∓30, ligula lineares, revoluti, apice subtruncati subintegrique. Flores tubulosi ∓24, corollarum lobis pappum paululum superantibus. Achaenia nitida, brunnea, oblanceolata vel anguste obovata, plana, marginibus crassiuscula, faciebus plerumque unicostata sed interdum costa mediana aegra vel etiam deficiente, glaberrima vel sparsissime longisetosa setis brunneis et valde adpressis, disco epigyno parvo onusta, corpore circ. 2 mm. longa; pappo albo vel sordido-albo, setis tenuissimis minutissime antrorso-hispidulis circ. 2.5–3 mm. longis.

Specimens examined: *Dr. William Hillebrand,* Waianae Mts., Isl. Oahu, Hawaiian Isls. (Herb. Berl.); *idem,* southeast slope of Mt. Kaala, Makaka, Waianae Range, Isl. Oahu, August, 1869 (Herb. Berl.; Herb. Bishop Mus.); *Dr. Heinrich Wawra* (*Voy. Donau*) no. 2290, Isl. Oahu, 1868–1871 (type, Herb. Mus. Vienna).

Tetramolopium rockii sp. nov.—Frutex humilis, erectus vel plus minusve depressus, 3–4.5 dm. altus, ramosissimus ramulis hispidulis supra confertissime foliosis. Folia spathulata, plana, crassiuscula, apice obtusa vel orbiculata, inferne sensim in petiolum validum rigidum subplanum marginatum hispido-ciliatum 4–8 mm. longum angustata, obsolete 1-nervia, faciebus rugoso-papillatis plus minusve hispidula glandulosaque, margine hispido-ciliata et integra vel apicem versus minutissime serratulata, 1–1.8 (rarius –2.7) cm. longa et 2–3.5 (rarius –6) mm. lata. Capitula solitaria circ. 1.2–1.5 cm. lata, pedunculis subvalidis hispidulis paucibracteatis ramulos terminantibus 5–12 cm. longis. Involucrum 5–6 mm. altum, bracteis numerosis oblongo-linearibus acutis extus glandulo-hispidulis. Flores ligulati 60–80, albidi, ligula tubo paulo breviore. Flores tubulosi numerosi, sicci subalbidi, corollarum lobis exsertis. Achaenia stramineo-fulva, obovata, plana, faciebus antrorsum adpresso-hispidula et perspicue uninervia, marginibus calloso-incrassata et aegre erecto-hispida, corpore circ. 2 mm. longa, pappo albo circ. 3 mm. longo.

Specimens examined: *Joseph F. Rock* 10299, on beach, Moomomi, Isl. Molokai, Hawaiian Isls., March, 1910 (type, Herb. Gray: cotypes, Herb. Berl.; Herb. Bishop Mus.; Herb. Field Mus.).

Tetramolopium lepidotum (Less.) comb. nov.; *Erigeron lepidotus* Less., Linnaea **6**:502. 1831; *Vittadinia chamissonis* A. Gray, Proc. Amer. Acad. **5**:119. 1861; *Tetramolopium chamissonis* Hillebr. Fl. Haw. Isls. 199. 1888.—The type material of LESSING'S species had been collected by *Von Chamisso* on the Island of Oahu, 1816–1817. LESSING mentioned having seen several of the dried specimens. The Berlin sheet is from KUNTH'S private herbarium and bears three specimens given to KUNTH by *Von Chamisso* in 1831. While any *Von Chamisso* material which might still be extant at Halle would by some be taken as the type, the Berlin sheet is thoroughly ample for all practical purposes. One specimen is the form described by LESSING for his *Erigeron lepidotus,* having "folia.....6–9‴

longa," and later described by ASA GRAY as *Vittadinia chamissonis*. The other two specimens are larger and have leaves 3–5.5 cm. long. These match the type material at Kew of *Erigeron pauciflorus* Hook. & Arn. and the type material in Berlin of *Tetramolopium chamissonis* var. *luxurians* Hillebr., and are to be distinguished varietally as:

TETRAMOLOPIUM LEPIDOTUM var. **luxurians** (Hillebr.) comb. nov.; *Erigeron pauciflorus* Hook. & Arn. Bot. Beechey's Voy. 87. 1832; *Tetramolopium chamissonis* var. *luxurians* Hillebr. Fl. Haw. Isls. 199. 1888.

TETRAMOLOPIUM HUMILE **sublaeve** var. nov.—A specie plurimis foliis sparsim et saepe irregulariter setosis vel etiam setis omnibus deficientibus glabratis sed minutissime glandulo-punctatis, pedunculis 3–6-congregatis in unico ramo differt.

Specimens examined: *The United States South Pacific Exploring Expedition under Captain Wilkes*, Isl. Hawaii, Hawaiian Isls., 1840 (type, Herb. U.S. Nat.: cotype, Herb. Gray).

ASA GRAY at first had recognized this in the herbarium as a variety but later included it as a variation in his original description of the species proper ("Variat foliis hirsutioribus vel subglabratis"). The habit of having several peduncles on each branch is, however, quite distinctive and may be relied upon to separate this variety, as also the next following variety, from the species itself.

TETRAMOLOPIUM HUMILE **skottsbergii** var. prim. nomin.; *Tetramolopium humile* var. *β*, Hillebr. Fl. Haw. Isls. 199. 1888; *Tetramolopium humile* f. *laxum* Skottsb., Meddel. Göteborgs Bot. Trädgård **2**:273. 1926 (*ex num. sed sine descript.*).—Planta plus erecta et saepe minus hispida. Pedunculi plerumque 3–6-congregati in unico ramo et breviores, capitulis minoribus, floribus paucioribus. Achaeniorum facies obscure uninerviae praecipue ad basim.

Specimens examined: *Charles N. Forbes* 848*H*, Humuula Trail to summit of Mauna Kea, Isl. Hawaii, Hawaiian Isls., June 14, 1915 (Herb. Bishop Mus.); *Dr. William Hillebrand*, Central Plateau, Isl. Hawaii (type, Herb. Berl.); *Albert S. Hitchcock* 14278, alt. about 11000 ft., loose lava, slope of one of the peaks, Mauna Kea, Aug. 22, 1916 (Herb. Bishop Mus.; Herb. U.S. Nat.); *Jules Remy* 244, Isl. Hawaii, 1851–1855 (Herb. Gray); *Joseph F. Rock* 8333, alt. 10000 ft., Mauna Kea, June, 1910 (Herb. Bishop Mus.; Herb. Field Mus.;

Herb. Gray); *Carl Skottsberg* 703, alt. 3000 m., Mauna Kea, Sept. 28, 1922 (Herb. Goth.); *United States South Pacific Exploring Expedition under Captain Wilkes*, Isl. Hawaii, 1840 (Herb. Gray; Herb. U.S. Nat.; *cum specie ipsa commixtum*).

Named in honor of DR. CARL SKOTTSBERG, Director of the Arboretum of Gothenburg, who had given particular attention to this form, even designating it (*loc. cit.*) f. *laxum*, but without description.

TETRAMOLOPIUM ARENARIUM **confertum** var. nov.—Ramosior ramulis plerumque sub 1 dm. longis. Folia 1.5–3 cm. longa et 3–5 mm. lata apicem versus utrinque saepe 1-dentata dente acri. Capitula conferta pedicellis non vel vix manifestis, demum 4–6 mm. lata, involucro 2.5–3.5 mm. alto.

Specimens examined: *Dr. William Hillebrand* and *Rev. J. M. Lydgate*, growing 2–4 ft. tall, Nohoananohea[1] near Waimea, Isl. Hawaii, December, 1872 (Herb. Bishop Mus.); *Lydgate, eodem loco et tempore* (type, Herb. Berl.).

TETRAMOLOPIUM CONYZOIDES var. **dentatum** (H. Mann) comb. nov.; *Vittadinia conyzoides* var. *dentata* H. Mann Enum. Haw. Pl. *sub num.* 203, Proc. Amer. Acad. **7**:173. 1867.

Tetramolopium arbusculum (A. Gray) comb. nov.; *Vittadinia chamissonis* var. *arbuscula* A. Gray, Proc. Amer. Acad. **5**:120. 1861; *Tetramolopium chamissonis* var. *arbusculum* Hillebr. Fl. Haw. Isls. 199. 1888.

TETRAMOLOPIUM CONSANGUINEUM **leptophyllum** var. nov.—Folia anguste linearia, utrinque saepe 1–2-denticulata dentulis digito parvo similibus ∓0.6 mm. longis, 3–4.5 cm. longa et 1–1.5 mm. lata.

Specimens examined: *The United States South Pacific Exploring Expedition under Captain Wilkes*, Waimea, Isl. Hawaii, Hawaiian Isls., 1840 (type, Herb. N.Y. Bot. Gard.: cotype, Herb. Gray, *cum specie ipsa commixtum*).

CHICAGO NORMAL COLLEGE

[1] Spelling taken from HILLEBRAND'S label in Berlin. LYDGATE'S spelling is Nohoananohae.

VEGETATIVE REPRODUCTION IN CAMPTOSORUS RHIZOPHYLLUS

ILDA MCVEIGH

(WITH EIGHT FIGURES)

Introduction

Although regeneration and adventive growth are familiar phenomena in plants, the tissues concerned have been studied in relatively few species. NAYLOR (**8**) presents an exhaustive review of the literature on these and allied subjects, and finds that in the species in which their origin has been histologically studied, new parts arise from embryonic or slightly differentiated cells. No clear evidence of any considerable loss of differentiation was found.

Among ferns many examples are known of the adventive origin of new individuals. Both sporophytic and gametophytic tissues are produced adventitiously by fern gametophytes (**5, 9, 10, 11**). The new structures formed by such plants must originate from parenchymatous or from embryonic cells, since these are the only kinds present.

New plants arise from buds formed on the leaves of *Phegopteris sparsiflora*, *Acrostichum punctulatum*, *Pteridium aquilinum*, *Aspidium filix-mas*, *A. spinulosum*, *Woodwardia radicans*, *Chrysodium flagelliferum*, *Asplenium bellangeri*, *A. bulbiferum*, *A. viviparum*, *A. platyneuron*, *Aspidium aculeatum*, *Ceratopteris thalictroides*, *Woodsia obtusa*, *Cystopteris bulbifera*, and *Diplazium celtidifolium* (**1, 2, 4, 6, 7**). In *Pteridium aquilinum*, *Aspidium filix-mas*, and *A. spinulosum* the buds appear very early on the petioles, before development of the blades and differentiation of the tissues have begun. In *Woodwardia radicans* and *Chrysodium flagelliferum* the buds appear at the tips of the arched leaves. The buds of *Asplenium bellangeri*, *A. bulbiferum*, *A. viviparum*, *Diplazium celtidifolium*, and *Cystopteris bulbifera* have their origin in single isolated epidermal cells of the leaves, or in single superficial cells of the young leaf before the differentiation of the epidermis.

In *Platycerium*, *Asplenium esculentum*, *A. platyneuron*, *Ophioglos-*

sum vulgatum, and *Woodsia obtusa* new plants arise from buds produced on the roots (**2, 7**). In *Platycerium* and *Asplenium esculentum* the apex of the root may be directly transformed into a leafy bud. The buds of *Ophioglossum vulgatum* have their origin in the segments cut from the apical cell of a root.

Aposporous prothalli or prothallus-like tissues are produced by *Phegopteris polypodioides*, *Athyrium filix-foemina*, *Lastrea pseudo-mas* var. *cristata*, *Scolopendrium vulgare*, *Dicksonia punctilobula*, *Polystichum acrostichoides*, *Asplenium platyneuron*, *Woodsia obtusa*, *Cystopteris fragilis*, *Osmunda regalis*, *Pteris cretica* var. *albo-lineata*, *Aspidium marginale*, and *Woodwardia virginica* (**3, 5, 7**). In most of these species the prothalli are formed from detached primary or secondary leaves, but in *Asplenium platyneuron*, *Woodsia obtusa*, *Aspidium marginale*, and *Woodwardia virginica* they are formed also from detached roots. In *Woodwardia virginica* the gametophytic tissue arises from single cells on the surface of the leaves, or from cells on the surface or near the surface of roots.

The adventitious structures of ferns, so far as has been reported, have their origin in parenchyma cells, epidermal cells (usually when young), or embryonic cells. The present paper reports the results of a detailed study of the origin of new plants in *Camptosorus rhizophyllus*.

Material and methods

Coiled tips of leaves of *Camptosorus* were collected near Columbia, Missouri, killed and fixed in Carnoy's fluid, carried through the customary paraffin technique, cut 8–10 μ in thickness, and mounted serially. Most of the sections were made in a vertical plane parallel to the longitudinal axis of the leaf; a few sections were made perpendicular to the longitudinal axis. The sections were stained in Delafield's haematoxylin. Leaf tips and embryonic plants were preserved in formalin-alcohol, and the externally visible parts studied with the binocular microscope.

Observations

Structure of leaf tips

The leaves of *Camptosorus rhizophyllus* are simple, evergreen, and somewhat coriaceous. All are more or less cordate at the base but vary from obtuse to acuminate at the tip. The first leaves of a plant

are usually obtuse, but in older plants the differently shaped leaves are formed apparently in no definite order. The leaves have the usual circinate vernation. The long acuminate tips remain coiled but the obtuse and acute tips soon straighten. All types of leaves bear spores. The sori are oblong or linear and are found irregularly scattered on either side of the reticulate veins; those next to the midrib occur singly and the outer ones are usually arranged in pairs. Indusia are laterally attached.

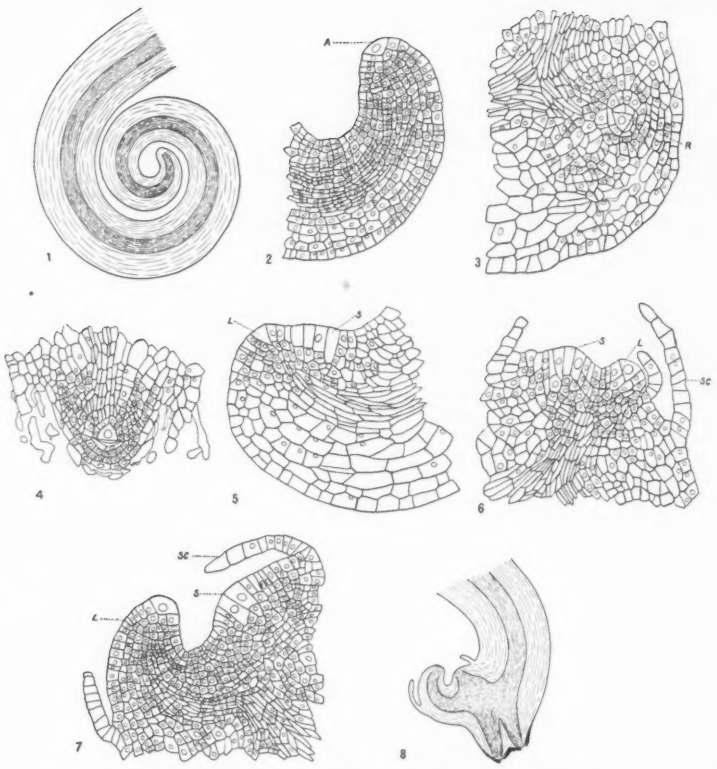
As the acuminate leaf tapers toward the tip it gradually changes in shape from a flat structure to one that is nearly cylindrical. Many glandular trichomes, each composed of three or four deeply staining cells, are found on the leaf near the tip.

Figure 1 represents diagrammatically the coiled leaf tip as seen in vertical longitudinal section. In figure 2 the extreme tip is represented in detail. The partially differentiated vascular tissue extends longitudinally through the center of the leaf almost to the tip. The cells on the inner (ventral) surface of the curve are small, their walls are thin, their nuclei are proportionally large, and they stain more deeply than the other cells of the tip. Many mitotic figures are found in this region. At the extreme tip and a little to the ventral side is a single large apical cell[1] (fig. 2). On its inner two faces are the cells which have been most recently cut off from it. The cells on the dorsal side of the leaf tip appear somewhat larger and more mature. A cross-section of the tip reveals the same difference between dorsal and ventral portions of the tip.

Formation of new plant

When the new plant is about to appear, the first change externally noticeable is in the shape of the parent leaf, which uncoils until only the extreme end is bent. This part of the leaf thickens and becomes somewhat club-shaped. Several slight protuberances are found on the surface of this structure. On the ventral surface is a relatively large rounded mass of tissue surrounded by scales. This is the apex

[1] Kupper (Flora **96**:361. 1906) has earlier discussed vegetative reproduction in *Camptosorus* (*Scolopendrium*) *rhizophyllus*. He states, "Die jungen Blätter verlieren sehr früh die Scheitelzelle und wachsen darauf mit Randzellen weiter." My investigation shows (fig. 2) that the apical cell not only persists until the leaf is mature but also (figs. 5, 6, 7) gives rise to the first leaf of the new plant. Kupper makes no statement concerning the plane in which his sections were made, and it is difficult to determine this from his figures.



FIGS. 1–8.—Fig. 1, diagram of vertical longitudinal section of leaf tip showing course of vascular strand. ×20. Fig. 2, vertical longitudinal section of leaf tip before vegetative reproduction has started (*a*, apical cell). ×110. Fig. 3, dorsal portion of vertical longitudinal section of leaf tip showing root primordium (*r*, apical cell of root). ×110. Fig. 4, longitudinal section through young root which has just broken through dorsal cells of leaf. ×110. Fig. 5, vertical longitudinal section through leaf tip in early stage in development of the first leaf and stem of the new plant (*l*, apical cell of first leaf; *s*, apical cell of stem). ×110. Fig. 6, ventral portion of vertical longitudinal section of leaf tip showing later stage in development of the first leaf and stem (*s*, stem tip; *sc*, scale). ×110. Fig. 7, ventral portion of vertical longitudinal section of leaf tip showing later stage in development of first leaf and stem of new plant (*l*, first leaf). ×110. Fig. 8, diagram of vertical longitudinal section of leaf tip which has started to develop into a new plant, showing vascular connections between parent leaf and parts of new plant.

of a new leaf; it is derived from the continued growth of the old one. On the lateral and dorsal surfaces are slight swellings, and the cells just beneath the surface in these areas are brown and apparently dead. In a later stage finger-like projections are visible on the sides where formerly the slight swellings were observed. These are roots which have forced their way through the outer cells of the leaf and are still surrounded by some of the dead surface cells which have not sloughed off. Their number, although variable, is usually five or six; those on the lateral surfaces appear first.

When the scales surrounding the bud are removed, the embryonic leaf and stem tip are visible on the ventral surface. The stem tip appears as a slight protrusion just proximal to the first leaf, a second embryonic leaf appearing lateral to the stem tip. Later the leaves arise on all sides of this tip. Only the extreme tip of the latter, well protected by scales and leaf bases, projects above the points of attachment of the leaves. The first leaves are small and usually somewhat obtuse, although their shape varies considerably. None of the first leaves remain coiled at the tip as do the older ones. The first leaf is the smallest. Well developed plants with several leaves and roots are found still attached to the parent leaves.

Sections through tightly coiled tips do not show the beginning of the growth of new parts; this is evident, however, in sections through tips that are beginning to uncoil. Vertical longitudinal sections are best for this study because of the dorsiventral orientation of the parts of the young plant.

Roots arise first in the ontogeny of the new plant. Development starts while the leaf tip is still somewhat coiled. In a section of a single leaf tip the roots are cut at different angles; this increases the difficulty of determining their origin. They arise endogenously and grow through the outer cells of the leaf tip in much the same manner as ordinary roots emerge through the cortex of a primary root.

It is probable that the first roots originate from cells in the embryonic region of the parent leaf tip. Figure 3 illustrates an early stage in the development of a young root. This root primordium is found in the embryonic region of the leaf tip just beyond the end of the procambial strand. The apical cell is discernible early in the ontogeny of the root. Some cells between the root primordium and

the procambial strand are still embryonic. It is possible also that roots originate in the procambium before the differentiation of the vascular tissues. It may be that the root initial is laid down at the same time as the cells of the procambial strand, or that one of the cells of the procambial strand becomes the root initial. The root initial thus formed may commence growth at once and so be of like age, in its development, with the terminal part of the leaf vein.

The young roots presumably force the outer cells of the leaf tip apart as they grow to the surface. Figure 3, which shows a cross-section through a young root, shows also the disorganized condition of the outer cells of the leaf tip caused by another root tip just dorsal to the one shown in the figure. Traces of the vascular strand and some of the outer cells of this root are also visible.

A median longitudinal section through a young root that has just broken through the epidermis of the parent leaf is shown in figure 4. At this stage the root apex is protected by a well differentiated root cap. Longitudinal and cross-sections of roots show that the growing point of the root is occupied by a tetrahedral apical cell. Cells are cut off successively from the four sides; those cut off from the distal side, which is usually somewhat more curved than the others, develop into the root cap. In this respect the roots resemble those formed normally from the stem of a fern.

Figure 5, a vertical longitudinal section through the tip, illustrates the origin of the first leaf. Instead of the single large apical cell which ordinarily occupies the tip of the leaf (fig. 2), there is a slight swelling, composed of embryonic cells, terminating in a small apical cell. This apical cell has the same shape as that of the parent leaf and occupies approximately the same position. The rate of cell division probably increases at this time, since the apical cell and the other cells of the new leaf surrounding it are smaller than those in the corresponding part of the tightly coiled tip. The first leaf of the new plant evidently originates from the apical cell of the parent leaf.

A later stage in the development of the leaf is shown in figure 6. The protrusion shown in figure 5 has increased somewhat in size. The apical cell is much larger in proportion to the surrounding cells than in the preceding figure, indicating that the increase in cell number is due more to the division of those cells formed by the apical

cell than to the division of the apical cell itself. The young leaf apex is protected by scales, which converge over it. These scales arise from the base of the bud.

Still another stage in the development of the leaf is shown in figure 7. The base of the leaf is thicker than the tip. Because the dorsal side enlarges more rapidly, the apical cell is forced to the ventral surface, and the tip becomes coiled.

The stem tip is located on the ventral surface of the parent leaf tip, proximal to the embryonic leaf (fig. 5). It appears first as a small protrusion separated from the embryonic leaf by a slight indentation in the surface. The cells in this indented portion are very small, while those on either side are actively dividing and enlarging. This is better illustrated in figures 6 and 7. The apex of the stem is occupied by a large initial cell which is much deeper than it is broad. In shape this cell resembles the segments cut off from the apical cell of the parent leaf. It is probable, therefore, that the stem originates from a segment of the apical cell of the parent leaf. In sections of older plants the stem tip does not protrude any more than in the figures just described. The roots, stem, and leaf and their relative positions are illustrated diagrammatically in figure 8. The vascular connections which soon arise between the new parts and the vascular bundle of the parent leaf are also illustrated.

The young plant formed by vegetative reproduction at the tip of the leaf is very similar (in, for instance, the stage illustrated in figure 6) to the embryo which results from syngamy. The shape of the first leaf and of the stem and their position with regard to each other are the same in both. The leaf apical cells of both are alike. The stem apical cells are alike, but differ from those of the leaves. The young plant which results from vegetative reproduction possesses several roots formed approximately at the same time and formed in the way later roots are formed on a plant, while the embryo has at first only one root. The roots of the two young plants resemble one another in structure, each having a single tetrahedral apical cell protected by a root cap. In the young plant produced vegetatively, nothing corresponding to a foot was observed. In this respect, it resembles embryos of apogamous origin (**10**).

Summary

1. The new plants formed by *Camptosorus rhizophyllus* arise in the embryonic region of the leaf tip.

2. The first leaf of the new plant is formed by the continued growth of the apical cell of the parent leaf.

3. The stem arises from cells in the embryonic part of the leaf tip, probably from one of the segments of the apical cell of the parent leaf.

4. The roots originate probably in two ways, from cells in the embryonic region of the leaf tip and from cells of the procambial strand.

5. In general, the condition in *Camptosorus rhizophyllus* is similar to that found in the majority of other species histologically studied, that is, adventitious structures have their origin in either undifferentiated or only slightly differentiated cells.

I wish to express appreciation to Dr. H. W. RICKETT and to Dr. E. E. NAYLOR for helpful advice and criticism during this investigation and in the preparation of this paper. Acknowledgment is due Miss CORAL FLEENOR for help with the illustrations.

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PHYSICAL LAWS AND THE CELLULAR ORGANIZATION OF PLANTS

R. B. THOMSON AND KATHLEEN L. HULL

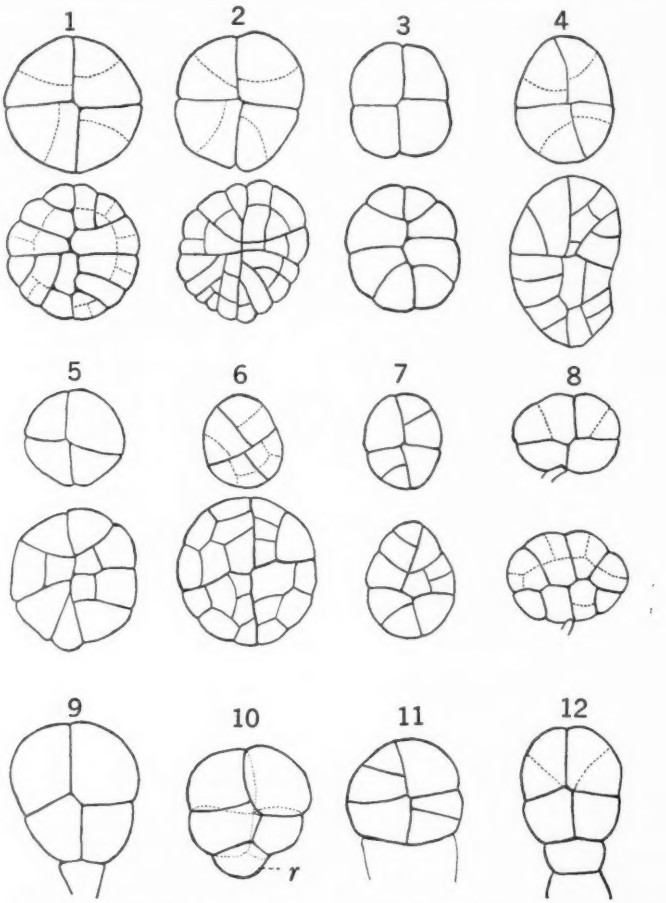
(WITH TWELVE FIGURES)

Since 1897, when ROUX (**5**) performed the experiments by which he demonstrated the essential similarity between a suitable system of oil drops and the early segmental stages of the egg of certain animals, there has been a sporadic but slowly growing interest in this field of research. The work of THOMPSON (**8**) has been perhaps the most stimulating. He demonstrated mathematically how the laws of minimum surface were applicable to stability of form. Two figures illustrating his theoretical requirements have been reproduced here (fig. 1). THOMPSON showed that the greatest stability in the quadrant aggregate was attainable when the members were asymmetrically arranged and there was a "dorsal furrow" (center of figure). At the third division a particular angle of anticlinal wall fulfilled the theoretical requirement (fig. 1, dotted line). When periclinal walls appeared in later stages these were accompanied by the more stable anticlinal type. The close correspondence between the theoretical requirements and actual organization was illustrated by THOMPSON in *Erythrotrichia* (fig. 2).

The applicability of these laws to the embryogeny of other animals was soon recognized, but it seems not to have been considered that the organizing tissues of plants might conform to such laws. This is possibly because a very thin and elastic wall is necessary for the fulfilment of the theoretical requirements, and a thick and firm wall is characteristically present in mature plant cells. Possibly also the widespread phenomena of filamentous growth in plants have been a deterrent factor, since the laws are applicable only to cells which have isodiametric symmetry, that is, are of spherical form.

Recently our attention was drawn to the possibility of the application of these laws to plants. In making a comparative study of embryogeny such uniformity was found in the cellular organization of the young embryo from bryophytes to seed plants that we were led to suspect that there was some fundamental factor involved. When

the forms of the cells were compared with the theoretical requirements, it was concluded that if the laws of minimum surface were applicable to the development of animals, they could also find applica-



tion to plants. Perhaps the reason for this is that the cells of plants may be spherical in form and thin walled while in the embryonic condition, and so can conform to the requirements as well as can those of animal cells.

After reaching the conclusion that the laws might apply to plants, many illustrations were found in the literature as well as in our own preparations. The tissues involved were from a variety of embryonic sporophytes and developing gametophytes, and indicated a wider applicability of these laws than had at first been suspected. This was made more evident by finding from our own material that drawings made in illustration of articles may be inaccurate and not represent the actual conditions. For example, the dorsal furrow may be omitted and the four cells represented as symmetrical. Often too the angle of anticlinal walls has not been properly drawn.

In order the better to direct attention to the applicability of these laws to plants, we have included outline drawings of the early cellular organization of a variety of forms. The figures are practically self-explanatory and only brief comments are needed. Figure 3 shows the organization of the teliospores of *Uredinopsis osmundae* drawn from a preparation made by Mr. S. M. PADY. In figure 4, stages of the sporophyte of *Targionia hypophylla* are illustrated (from CAMPBELL **2**). The drawings (fig. 5) of the young embryo of *Osmunda cinnamomea* are from our own preparations. Figure 6 illustrates the monocotyledon *Pistia*, while figure 7 shows the condition in a dicotyledon, *Acacia*, the former from HEGELMAIER (**4**) and the latter from GUIGNARD (**3**). In figure 8 the young gametophyte of *Angiopteris evecta* is illustrated from the recent work of SCHMELZEISEN (**6**). In this case the upper cells have developed in advance of the lower, owing, SCHMELZEISEN considers, to the differential influence of light. A rhizoidal outgrowth too has begun to develop from one of the lower cells.

Figures 1–8 illustrate masses of cells which have come immediately from the development of a single cell, either gametophytic or sporophytic. In many plants the spore or fertilized egg cell does not develop immediately into a solid mass, there being an intervening stage which is often filamentous. In this case the delayed massive stage may also show conformity with the theoretical requirements. Figures 9 and 10 illustrate this condition in two gametophytes (*Osmunda* and *Equisetum*, redrawn from CAMPBELL **2**). Figure 11 is of a proembryo of *Pinus* (after BUCHHOLZ **1**), and figure 12 of *Urtica* (after SOUÈGES **7**).

Although we hold no brief for the applicability of physical laws to either plant or animal organization, it is felt that there are possibilities in the application of these laws to plants which should not be overlooked. For example, in work on embryogeny we have found that the literature, especially that of vascular cryptogams, is pervaded by the idea that the initials of adult organs appear very early. Some investigators label even the quadrant cells, stem, leaf, root, and foot. Others see in certain suggestively shaped cells of the primary massive stage the definitive initials of the adult organs. This has led to much confusion over the allocation of different organ initials to the various segments of the proembryo, and many of the contradictory statements in the literature can undoubtedly be traced to the mistaking of these numerous spurious initials for the true ones.

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* We have not been able to consult ROUX's original work, but it and other literature dealing with the subject have been critically reviewed in JAMES GRAY's Textbook of experimental cytology (Cambridge University Press. 1931).

BRIEFER ARTICLES

STANDARDIZATION OF METHOD FOR DRAWING ALGAE FOR PUBLICATION

(WITH NINETEEN FIGURES)

Up to the present time no standard system of magnification in drawing algae for published articles has been adopted. A plan used in the phycological laboratory of the University of Minnesota is briefly described in this note.

Since most botanical journals and texts have pages measuring approximately 5×7 inches, a standard size of 4×6.2 inches has been adopted. This leaves space at the bottom of the illustration for the legend or explanation of the figures.

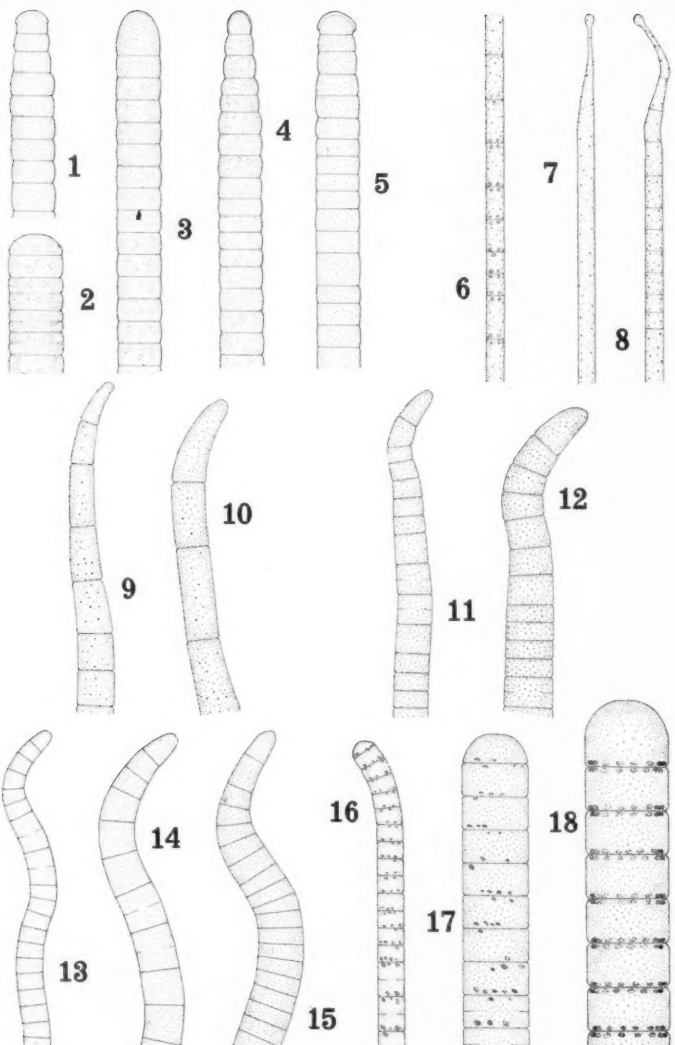
TABLE I

DIRECTION TO ARTIST		DIRECTION TO PHOTOGRAPHER	
DIAMETER OF CELL (μ)	AMOUNT OF MAGNIFICATION	SIZE OF SHEET (INCHES)	SIZE OF PRINT (INCHES)
1.0–3.5	1 μ = 10 mm.	20×31	2×3.1
4.0–9.5	1 μ = 5 mm.	20×31	4×6.2
10.0–24.5	1 μ = 2 mm.	8×12.4	4×6.2
25.0–75.0	1 μ = 1 mm.	4× 6.2	4×6.2

A micrometer eyepiece is necessary. The value of the scale divisions must be ascertained for the high power objective and eyepiece combination to be used. An oil immersion objective should be provided for objects less than 5 μ in diameter.

The first step in the process is to obtain the diameter in micra of one of the typical cells in the plant to be drawn. On the basis of this measurement a suitable factor for magnification of the object in the reproduction may be determined. The factors employed in this laboratory are given in table I.

In making the drawing, each true measurement must be multiplied by the proper factor. A cell measuring 3×5 μ would be drawn 30×50 mm. in size. In such a drawing all details may be properly brought out. Curved



FIGS. 1–18.—Species of *Oscillatoria:* figs. 1–5, *O. rubescens;* figs. 6–8, *O. splendida;* figs. 9, 10, *O. cortiana;* figs. 11, 12, *O. okeni;* figs. 13–15, *O. terebriformis;* figs. 16–18, *O. tenuis.* ×1000. (Drawn by MARJORIE A. FORBES.)

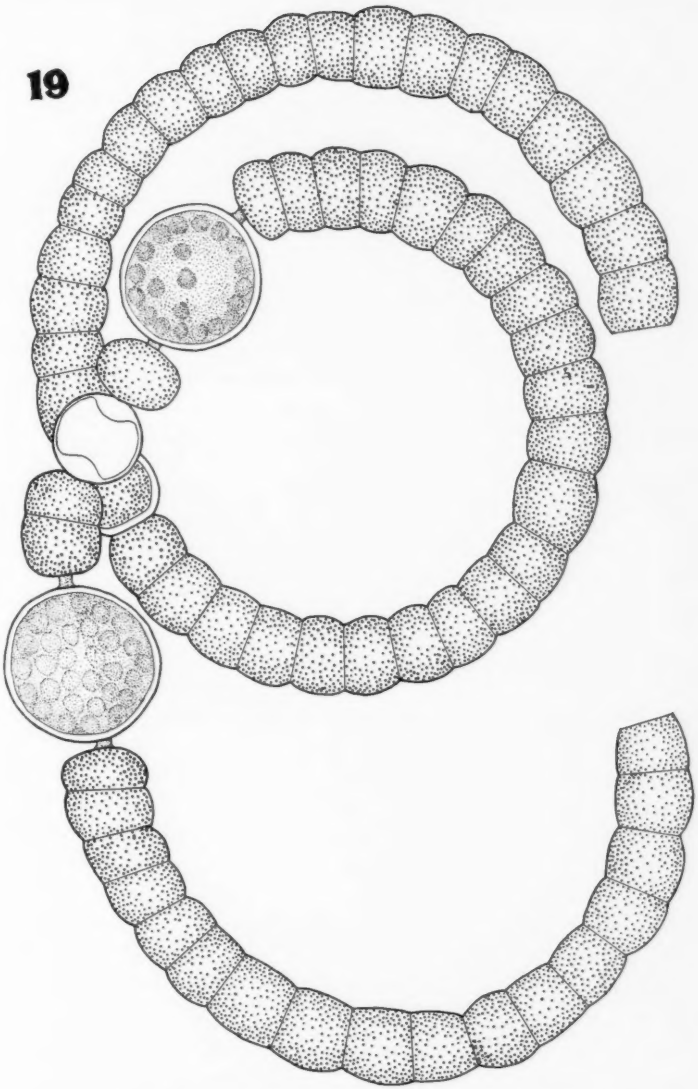


FIG. 19.—*Anabaena* species; a common "water bloom" alga. ×1000. (Drawn by MARJORIE A. FORBES.)

lines and tapered or hooked end cells may be exactly depicted. Finally, before being traced on a good grade of paper, the drawing must be checked by measuring longer distances between any two points here and there, as from the apex of the trichome to the base of the tenth cell, for example. A cell measuring 8 μ in diameter should be drawn 40 mm. wide; one measuring 20 μ should be drawn 40 mm. wide; while if the cell is between 25 and 75 μ in diameter, multiplication is unnecessary since the factor 1 is used.

The figures are now traced on drawing paper which will take India ink well. Pen points of the proper type[1] must be used for inking the drawings.

After the drawings are made they are cut out and attached, with rubber cement, to a sheet of firm white paper of the proper size, ready for the engraver. The sheets should be laid out very carefully with soft pencil lines setting off the margins. The space on the sheet inside the margin lines should measure exactly 20×31 inches, in case the factor 10 or 5 was used in drawing; 8×12.4 inches, with the factor 2; 4×6.2 inches, if the factor 1 was used. The drawings are now to be arranged as indicated by figures 1–19. They should be placed farther apart on the larger plates and closer together on the smaller ones.

In photographing the illustrations, care must be taken to have the sheets reduced exactly to certain diameters, according to the magnification used in drawing. In the objects multiplied by 10, the sheet, 20×31 inches, must be reduced to a print measuring exactly 2×3.1 inches. Four of these will make an illustration measuring 4×6.2 inches. If the object was multiplied by 5, the sheet, 20×31 inches, must be reduced to a print measuring exactly 4×6.2 inches. Likewise the sheet measuring 8×12.4 inches must be reduced to a print 4×6.2 inches in size. The result will be that, in every case, the figures on the published plates will represent a magnification of exactly 1000 diameters.—JOSEPHINE E. TILDEN, *University of Minnesota, Minneapolis, Minnesota.*

[1]

PEN POINTS TO BE USED FOR:	MAKE OF PEN POINT:
Factor 10	Esterbrook no. 788, oval point
Factor 5	Leonardt no. 516 E.F., ball point
Factor 2	Leonardt no. 516 E.F., ball point, or an old Gillotte no. 404
Factor 1	Gillotte no. 404 or Dietzgen no. 3440

CURRENT LITERATURE

Flora of the southeastern United States

In a long awaited and but recently published volume,[1] SMALL has presented a noteworthy treatment of "the species of nature and naturalized flowering plants known by the author to grow naturally in the southeastern United States south of the northern boundaries of North Carolina and Tennessee and east of the Mississippi River." These total 5557, distributed among 1518 genera and 233 families. The volume might pass for a much revised third edition of SMALL'S Flora of the southeastern United States, first published in 1903; it deals, however, with a more restricted area. Within the range covered, it easily eclipses all floristic works of the past and will doubtless be the commonly accepted authority for many years to come. In a general way the sequence of plant families is that employed in ENGLER and PRANTL'S Die Natürlichen Pflanzenfamilien. Conventionally enough, a logical English equivalent accompanies the scientific name of each family, such as, for example, Primrose Family for Primulaceae, and Gentian Family for Gentianaceae. For orders, however, there is used the quite different method of modifying the scientific name itself. Thus the Primulales are the Primulal Order, the Gentianales the Gentianal Order, etc. Pteridophyta are omitted. In numerous cases the descriptions have been abbreviated. A valuable feature is "a drawing showing a flower and its gross morphology and a fruit, of the first species under each genus given." The author disclaims (p. v) having been influenced in his treatments of the various groups by traditional "lumping" and modern "splitting." Generally speaking, however, the larger families and genera have been broken down into smaller groups, so that the subfamilies and generic sections of many authors are shown respectively as families and genera. Numerous sections of earlier authors have, moreover, been designated subgenera (e.g., *Eucorcopsis*, *Anacis*, *Silphidium*, and *Calliopsis*, p. 1446), thus further overloading our already heavily encumbered nomenclature without apparent gain to taxonomy. Further confusing the student, the status of subgenus is no sooner proposed than it is in various cases dropped or at least ignored and a new set of names given (e.g., Lanceolatae, Palmatae, Latifoliae, etc., p. 1446), without designated status, but intended manifestly as mutually coordinate and yet created in some cases for a subgenus and in others for a mere fractional group lower than a subgenus in rank. Too often distinctions relied upon for such appellations become wholly or in part obliterated as subsequent cosmopolitan monographs are produced. Hence, aside from the matter of needlessly dupli-

[1] SMALL, J. K., Manual of the southeastern flora. 8vo. pp. xxii+1554. Illustrated. Published by the author, New York (press of the Science Press Printing Co., Lancaster, Pennsylvania). 1933.

cating names or of forfeiting claims to consistency, it would seem that authors of manuals, dealing as these commonly do with more or less restricted ranges, should exercise the utmost reserve in the delimitation of sectional or other subgeneric groups.

Minor variations of species, "varieties" or "subspecies," are said in the preface not to have been considered to any great extent. It must be noted, however, that many of the "species" listed (e.g., *Euonymus obovatus*, p. 817; *Bidens nashii*, p. 1453; *Coreopsis crassifolia*, p. 1447; and *C. lewtonii*, p. 1449) are by various other authors construed as mere varieties. A short and all too inadequate appendix of 3 pages appears toward the end of the volume. Recording as it does but a small portion of the advances made since much of the manuscript was prepared for the press, it leaves the work as a whole somewhat out of date.

While students of the flora of the southeastern United States will find the volume none the less indispensable, the greatest importance which it will have for many taxonomists arises probably from the number of new genera and species and new combinations proposed. The new names alone cover seven pages (pp. 1503–1509), even though numerous technically new names or combinations for subgeneric divisions have been omitted. Descriptions of new species are given in English; in this and various other respects the International Code is ignored. As might have been expected in so large an undertaking, the revisional work upon several of the groups was done by assisting botanists, some of them specialists. Typographically, an exceptionally high standard of excellence has been attained throughout. It is to be hoped that this same standard will be maintained in the companion volume which the author proposes to produce later, dealing with the flora of the country adjacent to the west and extending to the western boundary of Texas.—E. E. SHERFF.

Cytology

The activity of recent years in the field covered by SHARP's[2] important text has necessitated another rewriting. Again the author has summarized a great amount of new material in masterly fashion, and has incorporated it with what went before into an effective unity. Those who make daily use of the results of his labors can but be grateful for the expenditure of time and energy involved in the digestion and organization of an enormous literature. Not only is it cytology proper (or cytology in the older sense) that he has had thus to summarize; preparation of the new edition, more so than in the case of the earlier ones, has required an equal familiarity with the work in experimental genetics. The magnitude of the task can be appreciated by those who find it a man-size job to keep up with the literature dealing with *Drosophila* alone.

A major problem of the author has evidently been to keep his book within the bounds set while including so much that is new. This is evidenced by the following list of new chapters, dealing with subjects not touched, or but very briefly

[2] SHARP, L. W., Introduction to cytology. 3d ed. pp. xiv+567. figs. 230. McGraw-Hill, New York. 1934.

treated, in the previous edition: morphology of the chromosomes; structure of the chromosomes; fragmentation and translocation; reciprocal translocation; heteroploidy; cytogenetics of autoheteroploid plants; cytogenetics of hybrids; cytoplasmic heredity. Also to be included, of course, were new results bearing upon virtually every topic previously treated. Yet the work has been kept within the compass of the previous edition; indeed, the number of pages is slightly fewer.

Many will regret the abridgment thus involved. Some of us would have been glad to see a fuller treatment of many topics and a retention of some discussions that have been deleted. This would have meant a volume of perhaps twice the present size, a volume beyond the reach of students, and probably one that could not be published in this country. But it would have been a better book, and one that only SHARP could write.

One is tempted to speculate as to whether the author did not sometimes question how far he need go in his exposition of the scientific heterozygote known as cytogenetics. He has gone, or so it seems to the reviewer, the full length. At the same time it is probably true that if the field was to be entered, the discussion could hardly have been much briefer. So many, so heterogeneous, and so unorganized as yet are the facts to be considered that a summary organization is out of question. Yet the space devoted is probably disproportionate to the real value of the facts at hand. Certainly the adequate treatment of cytogenetics has meant a less adequate, because greatly abridged, treatment of topics the present knowledge regarding which is probably in reality much more important.

Another problem inevitable in an up-to-date work inheres in the fact that very recent reports of results not yet tested or confirmed must be cited, and it is difficult to cite them at other than their face value. Here enter questions of opinion, and the critic must proceed cautiously. An illustration is the author's apparent acceptance of a few descriptions of the purely intranuclear origin of the spindle in the higher plants. This conception negatives the results of a great number of investigators whose conclusions are not necessarily to be discarded entirely because of their relative antiquity. More skepticism might have been justified in the treatment of some very modern papers dealing with this and other problems upon the basis solely of the Benda fixation. Many cytologists find the Benda fixative especially unreliable except for the purpose for which it was developed, namely, the demonstration of the chondriosomes.

The volume is an excellent and valuable contribution, and the cytological world is once more deeply indebted to its author.—C. E. ALLEN.

Kansas wild flowers

Situated between the regions of eastern and western floras, Kansas has had little in the way of manuals or floras for its students of native plants. This fact makes the recent publication[3] all the more welcome. The home botanist may

[3] GATES, F. C., Wild flowers in Kansas. Kas. State Board of Agric. Rept. **51**: 1–295. figs. 448. W. C. Austin, State Printer. Topeka.

now identify many of the plants of the prairie and the plain by the use of this non-technical manual. The task is made the easier by the many clear drawings. If the scale on which each drawing appears on the printed page had been indicated, it would have given the student a better idea of the proportionate size of the plants. The text abounds in keys to families, genera, and species. The classification follows the BESSEYAN system very closely and agrees with RYDBERG in the division of many old genera.

Instances of improved or reformed spelling appear on its pages. There seems no decided objection to "tootht," "brancht," and "groupt," but the use of "Alismataceae" for Alismaceae and "adder's-tung" for "adder's-tongue" will probably seem objectionable to many older botanists. But these are minor objections in a very creditable and useful book.—G. D. FULLER.

Flora of the grasslands

The forests of the east and the mountains of the west have for many years had adequate manuals for the study of their flora. The grasslands that lie between the forests and the mountains have remained comparatively unknown, however, largely because of the lack of anything comprehensive or complete in the way of a manual. A recent volume[4] has removed this deficiency, and once again the botanists are indebted to RYDBERG for undertaking this arduous but needed task. They will all regret that the author received not even the scanty reward of thanks for his labors, as he died while the book was in process of publication. Many will regard RYDBERG's final contribution to botanical science as perhaps his most valuable. In many respects this volume is superior to his Flora of the Rocky Mountains and Adjacent Plains.

In this book the author has apparently followed rather closely the International Rules, although his tendency toward dividing families and splitting genera and species is still in evidence. In addition to the usual collection of keys and descriptions, the present volume has over 500 small illustrations from drawings, which will aid in the identification of many species. The descriptions seem to be concise but adequate, quantitative data for size and number are abundant, ranges are given outside the area included in the manual, and the synonymy is rather complete.

The publishers' work has been well done; the printing is good and the thin paper used has prevented the volume from being too unwieldy.—G. D. FULLER.

Plant names

With the continued neglect of taxonomy in many modern botanical laboratories, BAILEY's recent book[5] should form a welcome addition to botanical bookshelves. In his well known, pleasing style, the author traces the binomial system of nomenclature from the time of LINNAEUS to the present. He also con-

[4] RYDBERG, P. A., Flora of the prairies and plains of North America. pp. vii+969. figs. 600. New York Botanic Garden. New York. 1932. $5.50.

[5] BAILEY, L. H., How plants get their names. pp. vi+209. figs. 12. Macmillan Co., New York. 1933. $2.25.

siders the regulations to be followed in applying names to the many new species that botanical explorations are bringing to light. These considerations are illuminated by appropriate illustrations drawn from his wide experience in this field. Similarly he solves certain intricate problems of synonymy in a demonstration of the working methods of taxonomists. While the book is primarily intended for the use of horticulturists and agronomists, it is equally suited to the needs of botanists who have little familiarity with the rules and usages of botanical nomenclature. A few hours' pleasant reading will clear up many confusing details. These problems include the pronunciation and meaning of hundreds of scientific names. There are a number of interesting illustrations from the herbals of the seventeenth century.—G. D. FULLER.

Principles of plant physiology

The second edition of RABER's volume[6] has just appeared. The text has been enlarged by fuller treatment at certain places, and by additional sections in cases where recent advances warranted the inclusion of new material. The literature lists have been revised to include recent papers and texts. The order of presentation has not been changed, and no new chapters have been added. The approach is through the chemical physiology of the organism, photosynthesis, nitrogen metabolism, respiration, etc. A feature which students will appreciate is the inclusion of photographs of contemporary plant physiologists of Europe and America. Errors which marred the earlier edition have been eliminated. It is a helpful text.—C. A. SHULL.

Recent literature on gymnosperms

Recently an interesting textbook of living and fossil gymnosperms[7] has appeared which seems to be a practical compilation for the use of students. The text is simple and clear and the illustrations instructive although somewhat primitive. The atlas contains 38 plates with figures which look like blackboard drawings. There is nothing original in the text nor in the figures. The bibliography is short and inadequate, consisting primarily of a list of other textbooks. The absence of such an important general text as CHAMBERLAIN's Living Cycads strikes the reader as rather strange. But on account of its simplicity the book recommends itself to the student of plant morphology.

Another publication from the field of gymnospermous plant morphology and taxonomy[8] deals with two Rhaetic-Liassic genera *Cheirolepis* Schimper and *Hir-*

[6] RABER, O. L., Principles of plant physiology. 8vo. pp. xvi+432. Macmillan Co., New York. 1933.

[7] BEAUVERIE, J., Les gymnospermes vivantes et fossiles. Cours de botanique professé à la faculté des sciences de Lyon. Text and atlas in two volumes. 4to. Bosc frères. Lyon. 1933.

[8] HÖRHAMMER, L., Über die Coniferen—Gattungen Cheirolepis Schimper und Hirmeriella nov. gen. aus dem Rhät-Lias von Franken. Bibliotheca Botanica No. 107. E. Schweizerbart'sche Verlagsbuchhandlung. 4to. pp. 33. Illustrated. Stuttgart. 1933. Mk. 22.

meriella Hörhammer. This investigation has been carried out in HIRMER's laboratory by one of his students. The cuticular analysis method was used and the following technique applied. The stone slabs containing the fossil plants were treated with Schultze's maceration solution. After about 12 hours the rocks had disintegrated to sand and the plants from the surface and the interior of the slabs were entirely preserved and could be seen floating upon the liquid. The description of the two genera and various species is based primarily upon the cuticle and upon the form of the vegetative and some reproductive organs as preserved in the rocks.—A. C. NOÉ.

Plant life through the ages

It is gratifying to see a second edition of SEWARD's latest work[9] appear only two years after the first one. As was to be expected, the new edition does not differ very materially from the first. There is a list of additional references and a few alterations and corrections throughout the text.

This volume promises to become the standard textbook of plant paleontology in the English language. New editions will always absorb the latest literature and keep the reader informed on the progress of the science. It is admirably fitted to be the indispensable manual of the student as well as of the teacher. It was originally intended to be a book for readers unfamiliar with paleobotany, but it will be read mostly by botanists and geologists who already have some acquaintance with the subject. For a novice's introduction to paleobotany the book mentions too many forms which could be understood only if they were accompanied by illustrations. It seems desirable, therefore, that the number of figures and plates be considerably enlarged. Even the teacher and student of paleobotany would be grateful for such an enrichment of the book.

The lucidity and beauty of the author's diction and the rich background of his information are bound to guarantee continued success for this extremely useful book.—A. C. NOÉ.

Origin of cultivated plants

A very comprehensive treatment of the origin of cultivated plants[10] divides the subject matter into two parts, one general and the other special in character. The former contains chapters on methods of phylogenetic research and on the differences between wild and cultivated forms. For the botanist it is rather novel to see under the section on phylogenetic research a subchapter on historical-philological methods and linguistics. The study of the origin and migration of plants cultivated by man is helped by an investigation of plant names in different languages.

Using the resources of botany, anthropology, and philology, a full account is given of the history of cultivated plants since Neolithic times.—A. C. NOÉ.

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[9] SEWARD, A. C., Plant life through the ages. 2d. ed. 8vo. pp. xxi+603. figs. 139. University Press. Cambridge; Macmillan, London. 1933. $8.00.

[10] SCHIEMANN, E., Entstehung der Kulturpflanzen. Handbuch der Vererbungswissenschaft. Vol. III. pp. ix+377. figs. 96. Borntträger, Berlin. 1932. RM 50.

Taxonomic studies

Two interesting monographs appeared recently, one of which deals with a subdivision of the genus *Veronica*[11] and the other with the geographical and morphological features of *Aster alpinus* L.[12]

Both papers show well the modern type of ecologic-taxonomic investigation.—A. C. NOÉ.

New paleobotanical series

The well known paleontological publication Palaeontographica has established a subdivision devoted exclusively to paleobotany. It is edited by MAX HIRMER in Munich and counts among its associate editors such names as PAUL BERTRAND, W. GOTHAN, T. G. HALLE, W. J. JONGMANS, R. KRÄUSEL, J. WALTON, H. WEYLAND, and G. R. WIELAND. Its first number[13] appeared recently and contains contributions by KRÄUSEL and WEYLAND on the flora of the Middle Devonian in Bohemia and by HIRMER on the reconstruction of *Pleuromeia sternbergi* and on the morphology of Lycopodiales in general. Text and illustrations are excellent but the price is too high.

Every volume of this section will comprise six numbers. Only original articles are to be published in this series. It promises to become a very important collection of valuable monographs. Section A is devoted to paleozoology. Formerly only one series existed which contained both lines of paleontology. In this common series 77 volumes have been published already and the enterprise is old and well established.—A. C. NOÉ.

Cultivated conifers

Any book from BAILEY'S pen commands the attention of both botanists and horticulturists, for no one is better able to speak with authority in the two fields. Within the pages of this new volume[14] the botanist will find a critical and able discussion of the principles of classification and their application to the two families of the conifers. Synonyms are given and many of the troublesome problems of nomenclature considered in detail. In addition there are good descriptions of the different species with a careful consideration of geographic range. The illustrations are useful and a number of the plates are from beautiful photographic studies.

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[11] HARLE, A., Die Arten und Formen der Veronica-Sektion Pseudolysimachia Koch auf Grund systematischer und experimenteller Untersuchungen. Bibliotheca Botanica No. 104. E. Schweizerbart'sche Verlagsbuchhandlung. 4to. pp. 86. Illustrated. Stuttgart. 1932. RM 47.

[12] ONNO, M., Geographisch-morphologische Studien über *Aster alpinus* L. und verwandte Arten. Bibliotheca Botanica No. 106. E. Schweizerbart'sche Verlagsbuchhandlung. 4to. pp. 83. Illustrated. Stuttgart. 1932. RM 38.

[13] Palaeontographica. Vol. LXXVIII. Section B. Paleophytologie. Edited by MAX HIRMER. Lieferung 1–2. E. Schweizerbart'sche Verlagsbuchhandlung. 4to. pp. 56. pls. 7. Illustrated. Stuttgart. 1933. RM 68.

[14] BAILEY, L. H., The cultivated conifers in North America. pp. ix+404. pls. 48; figs. 114. Macmillan Co., New York. 1933. $7.50.

Both botanists and horticulturists will be interested in the many varieties that are recognized and given brief descriptions. For example, not less than ten varieties of Colorado blue spruce are noted, while the different varieties of the Norway spruce number fifty. One is surprised to find how largely Japan and China have contributed to our cultivated trees.—G. D. FULLER.

British economic grasses

At best the identification of grasses is a matter of considerable difficulty. Especially is this true of those forms occurring as a part of grazed lands where frequently only vegetative structures are available for study. The present work[15] is based on a detailed examination of the internal structures of the leaves of all the chief species of British grasses, supplemented with a critical study of other vegetative characters of diagnostic significance. More than fifty species are illustrated and their pertinent microscopic characters enumerated. There are brief keys based on anatomical details and vegetative characters. It may not be too much to hope that there may be more contributions of similar kind.—E. J. KRAUS.

The genus Diaporthe

A recent volume by WEHMEYER[16] is a taxonomic treatment of the genus *Diaporthe* and its allied genera, *Diaporthopsis*, *Apioporthe*, *Diaporthella*, and *Cryptodiaporthe*. There are keyed and described 71 species of *Diaporthe*, 6 species of *Diaporthopsis*, 8 species of *Apioporthe*, 3 species of *Diaporthella*, and 19 species of *Cryptodiaporthe*. One section of the volume is devoted to doubtful species of these genera, another to excluded species, and a large section to species not seen. The volume should prove of interest and use, not only to mycologists, but to pathologists interested in the diseases incited by the perfect and imperfect stages of the ascomycetes treated in this volume.—G. K. K. LINK.

Phytopathological and botanical research methods

The volume by RAWLINS[17] on phytopathological and botanical research methods is a contribution to botanical teaching and research which will be welcomed by all who attempt either the teaching or the learning of current phytopathological technique.

The volume deals essentially with microbiological techniques applied to phytopathogenic viruses, bacteria, and fungi. In addition to the microbiological, the book deals briefly with histological, microchemical, and biometrical techniques. Possibly this is the reason for the phrase "botanical research methods"

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[15] BURR, SYDNEY, and TURNER, DOROTHY M., British economic grasses: their identification by the leaf anatomy. pp. 94. figs. 111. Arnold & Co., London; Longmans Green, New York. 1933. $3.75.

[16] WEHMEYER, L. E., The genus *Diaporthe Nitschke* and its segregates. pp. vi+349. pls. 18. University of Michigan Press, Ann Arbor. 1933.

[17] RAWLINS, T. E., Phytopathological and botanical research methods. pp. ix+147. figs. 3. J. Wiley & Sons, New York. 1933.

in the title. Unfortunately one misses a chapter devoted to the techniques used in studying the rôle and influence of internal factors or of non-living environmental factors as direct and indirect pathogenic factors in non-infectious diseases; or of the indirect rôle and influence of internal as well as living (aside from the rôle of insects in virus diseases) and non-living external factors in infectious diseases. Possibly obligatory limitation of size of the volume demanded omission of these basic phytopathological techniques.

The growing field of virus diseases is recognized by a brief chapter. The bibliography of 960 titles is a valuable addition to the volume.—G. K. K. LINK.

Tradescantia

A brief volume has just appeared[18] in which is reviewed the rôle that the cells of *Tradescantia*, notably those of its stamen hairs, have played in the study of phytocytological problems during the past hundred years. Recent observations of the author are referred to, with a promise of more detailed discussion later. The recent literature is reviewed more exhaustively than the older, the former furnishing the key to the latter in so far as this is not listed. The review focuses attention upon the fact that *Tradescantia* cells have been used to a truly amazing extent in the study of nuclear, chromosomal, cytoplasmic, membranal, vacuolar, explantational, and other cellular problems.—G. K. K. LINK.

Dictionary of horticulture

Horticulturists and botanists alike will welcome this reissue of Hortus.[19] Here in a single volume is an annotated inventory of the main varieties of plants now in more or less general cultivation in the United States and Canada. Although the references are brief, they provide a wealth of helpful information with respect to methods of cultivation and nomenclature, which follows the system of the International Rules of 1905 and 1910.

It is the expressed hope of the authors, in which they will certainly be joined by all who must deal with cultivated plants, that volumes similar to this one will be revised, brought down to date, and reissued frequently. No other adequate method exists whereby an account may be kept of the cultivated flora.—E. J. KRAUS.

Virus diseases

The study of the effects of viruses in plants has led to such an abundance of empirical data that a summary statement has become necessary. In a recent volume[20] SMITH and BROOKS have ably assembled and summarized the enormous

[18] KÜSTER, ERNST, Hundert Jahre *Tradescantia*. pp. 36. figs. 7. Fischer. Jena. 1933.

[19] BAILEY, L. H. and ETHEL Z., Hortus: a concise dictionary of gardening, general horticulture and cultivated plants in North America. pp. 652. pls. 16; figs. 22. Macmillan Co., New York. 1930. Reissued 1934 at reduced price of $5.00.

[20] SMITH, K. M., and BROOKS, F. T., Recent advances in the study of plant viruses. pp. xii+423. figs. 67. P. Blakiston Son & Co., Philadelphia. 1934.

body of literature, much of it contradictory, which has grown out of the study of the diseases incited in plants by the invisible, supposedly living, agents which are designated as viruses. The volume should prove of great use to investigators in the field of virology as well as to phytopathologists and botanists in general. Some clarifying discovery and unifying generalization are necessary to bring out any underlying and hidden relations that may pertain to virus diseases and their incitants. The authors are fully aware of this, stating: "Not much further progress is likely to arise from continued study of symptomatology to which too much attention has been given in the past." It is not so much that excessive attention has been given to this phase, but rather that not enough attention has been given to other aspects of the problem.—G. K. K. LINK.

Recent advances in plant physiology

The necessity of printing a second edition of BARTON-WRIGHT'S[21] summary of progress in plant physiology in recent years attests its usefulness and popularity. There are some changes in organization, and some omission of material formerly included. The soil relations have been practically omitted, and there are now nine chapters instead of six, mainly because growth phenomena are given three chapters instead of one. The chapter headings are as follows: absorption of water and transpiration; carbon assimilation; nitrogen metabolism; the raw materials of plant nutrition; translocation; respiration; growth (three chapters). The revision has been accomplished with a slight reduction in the size of the volume.

It is a well written account of the recent progress in this field, and will be especially useful to students who need assistance in following the general trend of development of the subject, and in gaining a critical viewpoint with reference to recent work. The former edition won a wide circle of friends for the gifted young author, and these friends will welcome and extend the use of the new edition. —C. A. SHULL.

SIXTH INTERNATIONAL BOTANICAL CONGRESS

Amsterdam, September 2–7, 1935

The Organizing Committee of the VI International Botanical Congress has been asked to change the dates of this Congress. The Committee has now decided that the Congress will meet at Amsterdam (Holland), September 2–7, 1935.

A first notice regarding this Congress has been sent out to a number of addresses; for additional copies apply to the secretary, Dr. M. J. SIRKS, Wageningen, Holland.

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[21] BARTON-WRIGHT, E. C., Recent advances in plant physiology. 2d ed. 16 mo. pp. x+341. figs. 54. P. Blakiston Son & Co., Philadelphia. 1933. $4.00.